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The impact of climate change on the distribution and conservation status of African antelopes

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by Benjamin Luke Payne

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1. Introduction

Since life evolved on Earth there have been threats to biodiversity. Over the aeons the planet has experienced five mass extinctions resulting in losses of up to 96% of species on the planet at any one time (Barnosky *et al.*, 2011). The causes of past extinctions are believed to include volcanism and meteorite strikes that have led to changes in atmospheric gases and climatic change. Currently the Earth is witnessing a period of species extinctions that is higher than the background rate (Barnosky *et al.*, 2011) and could, if it continues, be the next mass extinction. What is unique about the current extinction episode is that it is caused by a resident species.

There is little debate among the scientific and conservation community about the negative influence of humans on ecosystems and that biodiversity faces threats from multiple fronts. From local to global scales, humans are affecting the ecological functioning of the planet (Sanderson *et al.*, 2002). Human population expansion, and consumption of resources, continue to grow as biodiversity suffers with a recent report suggesting a 52% decrease in vertebrate wildlife populations between 1970 and 2010. The Earth is no longer able to support the demands that humans are placing on nature with an estimated 1.5 Earths required to meet the current demand (WWF, 2014). The Millennium Ecosystem Assessment (MEA, 2005) provides an evaluation of the impact on global ecosystems over the past 50-100 years, and the current trends of the threats (Figure 1-1 redrawn from MEA, 2005). Figure 1-1 shows five drivers of change. Habitat change, invasive species, overexploitation, and pollution have all had very high impact on species over the last century in one or more habitats, whereas climate change (CC) has generally had a lower impact to date. However, the MEA (2005) report predicts that CC will be the "dominant direct driver of biodiversity loss" by the end of the 21st century. Furthermore, across all ecosystems, the trend is for a "very rapid increase in the impact" of CC on those ecosystems (MEA, 2005), and there is already growing evidence of species being affected by CC (Lenoir & Svenning, 2013; Cahill *et al.*, 2012; Hickling *et al.*, 2006; Parmesan, 2006).

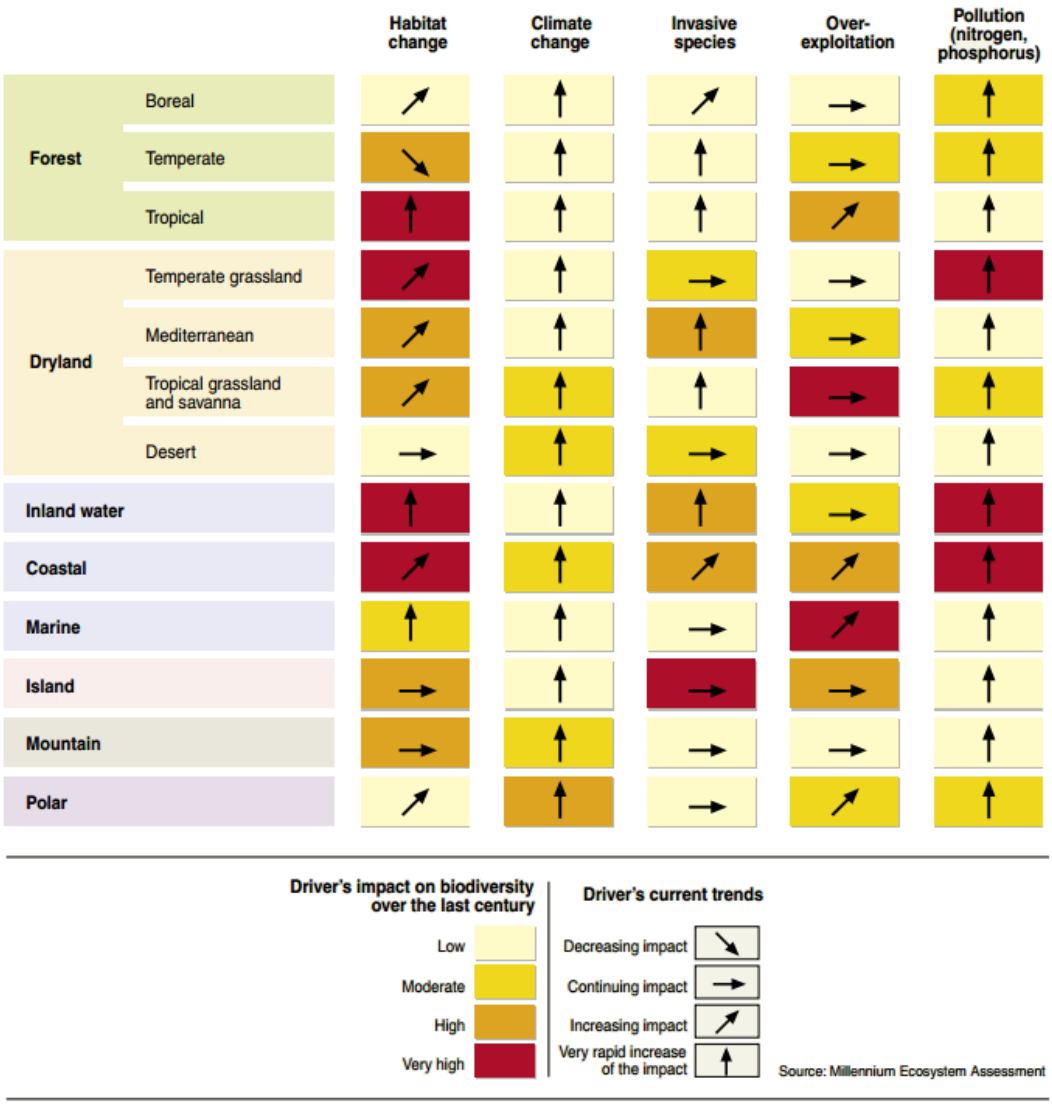

Figure 1-1: Five drivers of change for biodiversity and ecosystems. The impact of change relates to the past 50-100 years for each ecosystem. The arrows highlight the trend for each driver related to that ecosystem. Redrawn from MEA, 2005

While there is little remaining doubt that the Earth's climate is rapidly warming (IPCC, 2013a; Javeline *et al.*, 2013; Anderegg *et al.*, 2010; IPCC, 2007; New *et al.*, 2002), debate continues as to the exact cause of the warming. However, 97-98% of climate researchers believe the cause to be largely anthropogenic in origin (Cook *et al.*, 2013; Anderegg *et al.*, 2010). Current climatic change is linked to rising greenhouse gases (GHG) levels, such as carbon dioxide (CO_2) and methane (CH_4), being influenced by humans (IPCC 2007). Levels of GHGs have dramatically increased since industrialization and evidence suggests this rise is continuing. Atmospheric CO_2 levels have passed 400ppm[3] (Jones, 2013), up from pre-industrial levels of 280ppm[3] (Florides & Christodoulides, 2009; Hofmann *et al.*, 2009), and higher than the

natural range of the past 650,000 years (Siegenthaler *et al.*, 2005). There are many challenges in quantifying the severity of the change that have led to various climate scenarios being developed which suggest different future climatic conditions. These rely on differing assumptions about levels of emissions, and other variables (IPCC, 2013a). CC is therefore a global problem requiring a cohesive worldwide response. International targets have been set, such as limiting warming to 2°C above pre-industrial levels, but temperatures currently continue to increase in-line with the highest of the emission scenarios (A2 and RCP8.5) (Peters *et al.*, 2013). Changes in climate have an impact on biodiversity with the potential to affect all levels of biological organization from individuals, through populations, communities, ecosystems, and biomes (Woodward *et al.*, 2010). Furthermore, the present-day changes in CO_2 levels also provide a link between current climatic conditions and conditions experienced during previous mass extinctions (Barnosky *et al.*, 2011) prompting concern for all species.

While the Earth is globally affected by CC, some areas are expected to be more adversely impacted. Africa has been highlighted as an area of high vulnerability to CC and climatic variability (Boko *et al.,* 2007). Research into CC and its impact on past, present, and future climatic conditions in Africa, have been ongoing for many years (Hulme *et al.*, 2001). Large continent-wide climate changes are predicted, as is the evolution of novel climates, and the loss of current climates (Williams *et al.*, 2007). The vulnerabilities to CC in Africa include the water balance, agriculture, ecosystem change, human health, and the economic sector in general. Africa is also projected to see a large increase in human population, from one billion to potentially four billion by the end of the century (United Nations, 2014). The vulnerabilities to CC are influenced by the rise in population (Boko *et al.*, 2007). Increases in agriculture and livestock to support a larger human population will intensify environmental degradation and reduce biodiversity (Boko *et al*., 2007). Africa's biodiversity is also under increasing pressure from bushmeat hunting; a threat also linked to a growing human population (Lindsey *et al.*, 2013). To better understand the threats facing Africa's biodiversity it is important to examine how species are affected by CC and their possible responses to it. One method of achieving this is to model species current and future distributions by applying different future climate scenarios (Araújo *et al.*, 2005). This helps us to identify species of concern due to CC and gives us input into how they may be affected by other threats.

The following sections of this introduction provide a background to the project and the approach taken. Firstly, I review the impact that climate change can have on species directly,

through physiological stress, indirectly, through behavioural/phenological changes, or through changes to biotic interactions. In the following section I explain species distribution models, the most common method for predicting species distributions based on future climate projection. I explain the many options and subtly different methods, I also review the criticisms species distribution models have faced, and the arguments for their use. The next section introduces the model system, that of Africa's antelopes. Here, I describe the role of antelopes as part of a healthy ecosystem, and their importance to humans. This is followed by the potential responses that antelopes may have to climate change including spatial, phenological, evolutionary, and extinction. Climate change is one of many threats facing antelopes in Africa and a review of these additional threats is presented in this section. Finally, I describe the options for biodiversity conservation. I briefly review the history of conservation, the key organizations, the current targets, and the options available via *in-situ* or *ex-situ* projects.

How does climate change directly and indirectly affect species?

There are many ways in which climate change may affect species in the wild. Climate change influences both abiotic and biotic factors that have the potential to cause decline or extinction of populations and species. The abiotic factors can be further divided into those whose effects depend on physiological tolerances such as the temperature and precipitation, and those climate driven abiotic factors such as the increase in fire frequency, the loss of ice-caps, and rising sea levels (Cahill *et al.*, 2012). Changes in temperature and precipitation may affect species both directly and indirectly. Increased physiological stress may directly lead to an individual's death or the increased susceptibility to disease. Indirectly, species may be forced to seek refuge from high daily temperatures thereby restricting foraging time (Cahill *et al.*, 2012). In addition, hotter temperatures may decrease activity, and increase maintenance costs through thermoregulation (Kearney *et al.*, 2009). Furthermore, temperature changes may cause changes in fecundity and, in specific cases, sex ratios brought about by temperature-dependent sex determination (Foden *et al.*, 2009).

Even if a species has tolerance to local changes in climate, other species it relies upon may not. Cahill *et al*. (2012) separate these biotic factors to highlight the "negative impacts on beneficial species" and the "positive impacts on harmful species". Negative impacts on beneficial species include the reduction in prey, forage, hosts (for parasites), and symbiotic mutualist species such as pollinators. Positive impacts of harmful species relate to increases in predators, competitors, pathogens, and introduced species. Therefore, any changes to

biotic interactions such as habitat and forage, predator/prey, parasite/host, and mutualist (such as pollination loss) relationships all have the potential to affect the viability of populations (Cahill *et al.*, 2012; Foden *et al.*, 2009). Underlying some of these negative effects on species are phenological changes that interacting species display. This is particularly evident in plant species where changes in climate cause related changes in phenology and timing of annual biological processes. Most highly documented are the advances in spring 'tree leaf-out' events in temperate forests, however, changes have been witnessed from alpine tundra to tropical forests to subtropical deserts (Richardson *et al.*, 2013). Such changes can lead to temporal trophic mismatches between species. These mismatches have been recorded in many species and occur when one species that relies upon another as a resource such as prey, forage, pollination, or as a host, responds to a change in climate, but the other does not (Visser & Both, 2005). An example of this is the aforementioned changes seen in temperate forests where elevated spring temperatures cause earlier budburst in oak trees (*Quercus robur*). This phenological response by the oak trees may be matched or exceeded by winter moth (*Operophtera brumata*) egg hatching that feed on the oak. Great and blue tits (*Parus major* and *P. minor*) rely on the winter moth caterpillars to feed their young (Buse *et al.*, 1999). Intraspecific differences have been seen with some tit populations advancing their laying date while others have not (Charmantier *et al.*, 2008). Any mismatch with the direct food source timing results in reduced fledging success (Visser & Both, 2005).

While many of the long-term studies on trophic mismatch have concentrated on avian species, there is evidence that other groups, such as large herbivores, are also negatively impacted. For example, caribou (*Rangifer tarandus*) migrate to areas of highly nutritious food prior to lactation to ensure milk production for their offspring. Studies demonstrate that climate change has led to "spatial variability in plant phenology" in some areas. This has led to reduced offspring survival because the available plant resources are (a) smaller; and (b) available for shorter periods as flowering, fruiting, leaf opening periods are reduced (Post & Frochhammer, 2008; Post *et al.*, 2008).

Changes in vegetation phenology can also have wider ranging consequences on the nutrient and carbon cycling processes, and these have the potential to influence entire communities of species (Richardson *et al.*, 2013). Species can therefore be affected by CC in multiple ways, but this raises the question of what makes a species vulnerable to climate change. Over 90

traits have been identified that relate to species susceptibility. These have been grouped into five trait groups (based on Foden *et al.*, 2009):

1. *Specialized habitat and/or microhabitat requirements (e.g. cave-dwelling species, or plants that require specific soil types)*. Where species requiring specialist habitats are able to disperse they are less likely to find suitable habitat than habitat generalists. Those species where the habitat itself is threatened, such as polar or mangrove, may be doubly threatened.
2. *Narrow environmental tolerances or thresholds.* Physiology and ecology are closely linked and result in specific climatic niches for each species. Species with a narrow niche are more likely to be pushed beyond that niche by smaller fluctuations than those with broader niches. However, it is still possible that a species with wider ecological tolerances may be pushed beyond their limits.
3. *Poor dispersal or colonization ability.* Species dispersal varies greatly by taxa and species characteristics such as generation time, ecology, morphology, and fecundity (Dawson *et al.*, 2011; Schloss *et al.*, 2012). Dispersal due to climatic change is not unique to present day, however, fragmented landscapes and human dominated areas present new challenges to dispersal.
4. *Dependence on specific environmental triggers or cues.* Migration, egg laying, hibernation, breeding, and seed germination all have the potential to be affected by CC. As established above, this can lead to a temporal mismatch in timing with essential resources.
5. *Dependence on interspecific interactions*. While the focal species may not be directly affected by CC, interacting species may be which may in turn impact on the focal species. This may be the result of a temporal mismatch as above; alternatively it may be due to the loss of those interacting species through extinction or dispersal. Commensal and closer tied species will be at greater risk.

Whether CC can cause extinction due to physiological limitations is unclear for most species. Still, it is thought that the disruption of interactions between species may be a more important cause of extinction in the future (Cahill *et al.*, 2012).

Species distribution modelling

Identifying how species distributions may be affected by CC will give us clearer understanding of which species are negatively impacted or threatened by a changing climate. Species distributions are largely determined by climatic factors (Schloss *et al.*, 2012; Parmesan &

Yohe, 2003; Beerling *et al.*, 1995; Janzen, 1967; Hutchinson, 1957; Grinnell, 1917) that interact to produce a species' climate niche. The climatic niche represents the fundamental niche, or where a species can potentially occur. However, there are other abiotic factors that may contribute to a species' fundamental niche such as light, edaphic conditions, slope, and aspect (Wright *et al.*, 2006; Silvertown, 2004). Other factors then forge a species' realized niche, that being the part of the fundamental niche that is occupied (Quintero & Wiens, 2013; Pearson & Dawson, 2003). These factors are largely biotic interactions divided into positive (e.g. pollinators, seed dispersal, suitable forage/prey) and negative (e.g. predation, competition including invasive species, disease, unsuitable habitat) (Soberón & Peterson, 2005). Further considerations that contribute to the realized niche include natural barriers to dispersal, dispersal ability and velocity, and the evolutionary ability of a species to adapt to new conditions (Soberón & Peterson, 2005; Pearson & Dawson, 2003).

The knowledge that species distributions are broadly based on climatic variables has presented the opportunity to model those distributions. Climate envelope models (CEMs; or bioclimate envelope models) are correlative models that express species' observed distributions based on a 'multivariate space of climatic variables' (Araújo & Peterson, 2012). CEMs are often used as a synonym for species distribution models (SDMs), ecological niche models (ENMs), and habitat suitability models. However, there is debate over the differences between model types. SDMs can be said to incorporate CEMs, where SDMs may include additional abiotic variables. In the strict sense, neither CEMs nor SDMs include biotic interactions or species dispersal as part of their models (Araújo & Peterson, 2012). ENMs seek to incorporate abiotic variables and ecological niche theory (Peterson & Soberón, 2012; Elith & Leathwick, 2009) which many consider to be a representation of the realized niche (see Araújo & Guisan, 2006), however, others consider it to be closer to the fundamental niche (Soberón & Peterson, 2005). Habitat suitability models include biotic interactions and resources utilized by a species, and aim to identify areas of suitable habitat for a species rather than the actual distribution (Araújo & Peterson, 2012). Despite these distinctions, many authors continue to include all modelling options as either SDMs or ENMs (Peterson & Soberón, 2012).

As noted above, there is debate on whether the fundamental or realized niche is being modelled using the different methods. Pearson and Dawson (2003) highlight that correlative models such as CEMs are based on the realized niche rather than the fundamental niche because they reflect a species' known distribution as influenced by additional biotic and

abiotic factors. This is key to understanding the models uses and limitations. The realized niche is a subset of the fundamental niche (Soberón & Nakamura, 2009), therefore, climatic conditions within the realized niche are likely to be representative of the entire fundamental niche. This is because it is assumed that the factors restricting a species from being present are not climate related. In this way CEMs predict the fundamental niche based on the realized niche. However, this depends on the degree to which the realized niche is restricted by non-climatic factors. If the realized niche is not greatly influenced by non-climatic factors, then there is a greater chance that the species will be present in areas fully representative of all climatically suitable conditions for that species. This being the case, the model will represent the fundamental niche more closely. Similarly, CEMs may indicate areas that are climatically suitable, but not populated by the species being modelled. Where this occurs the model is considered to have reduced sensitivity and specificity (number of correctly predicted presences and absences respectively), because areas are unpopulated due to non-climatic factors mediated through abiotic or biotic interactions (Guisan & Zimmermann, 2000). From this it is clear that any past or future predictions based on the CEMs, will suggest these areas as suitable based on climate alone. This presents an alternative use for CEMS where it has been possible to identify areas which are climatically suitable that may contain undiscovered populations (Särkinen *et al.*, 2013).

CEMs, can be used to predict the past or future distribution of a species based on historic or projected climatic conditions. While the other modelling options also allow this, they include additional variables. These additional variables must also have projections associated to them, or they should be static. For dynamic abiotic variables, such as edaphic conditions, this adds an additional level of uncertainty to the predictions produced using the models. The same applies to models incorporating biotic interactions or habitat suitability where projections for other variables may also be required or desirable. This does not suggest CEMs are better suited to predicting species future ranges, but that the uncertainty inherent in other approaches needs to be acknowledged.

Scale is an important factor when considering modelling approaches and the variables they are based upon. Different processes act at different scales. Therefore, at a coarse spatial scale, abiotic variables such as climate and topography reliably predict species presence. Whereas, at a finer scale, additional processes, such as land use, edaphic qualities, and biotic interactions, are required to further assess the presence of a species (Soberón, 2007;

Pearson & Dawson, 2003). The goal of the study, the species in question, and the availability of data at a given scale will influence which variables to include.

When predicting the future distribution of species, SDMs and CEMs typically fail to include the dispersal potential of the species (Travis *et al.*, 2013; Araújo & Peterson, 2012). SDMs can be extended to include dispersal. In the past this has often involved an 'all or nothing approach' whereby a species is unable to disperse or able to freely disperse to all suitable areas regardless of biotic or abiotic barriers (Franklin, 2010; Thuiller *et al.*, 2006a). This provides the "two extremes" in terms of dispersal (Araújo *et al.*, 2006), and has been described as offering pessimistic and optimistic viewpoints (Markovic *et al.*, 2014). However, free dispersal to all areas, potentially globally, is unrealistic rather than optimistic. The inclusion of improved dispersal modelling has been advocated as an important step in bringing realism to model based predictions of species distributions in the face of climatic change (Thuiller *et al.*, 2008). Dispersal is poorly understood for most species, however, recent studies have provided models that predict dispersal velocity for a number of taxonomic groups, such as mammals. Schloss *et al*.'s (2012) model, based on mass and diet, provides a yearly dispersal velocity. Such models may be criticized as overly simplified, but they provide the opportunity to integrate dispersal into SDM projections in light of species specific data.

Dispersal velocity is only one component of understanding whether a species can reach new areas within a given timeframe. Suitable habitat in adjoining areas, human and natural barriers, and contiguous climatic conditions need to be considered. This need for contiguous climatic conditions through time may be overlooked in modelling. A CEM or SDM may predict suitable climatic conditions in the future that are far removed from the existing distribution and that do not have suitable climatic conditions linking those areas. However, in these cases it is unclear if the areas between the current and predicted distributions had suitable conditions during the intervening period. An *a priori* assumption may be that suitable climatic conditions for a species simply shift over time due to CC thereby allowing dispersal. However, CC is likely to be responsible for the loss of climates and eruption of global and regional novel climates (Williams *et al.*, 2007). There is therefore potential for unseen climatic barriers to dispersal between areas of climatic suitability. In addition to these barriers there are other potential biotic barriers such as predators, competition, missing symbiotic species, and novel diseases which provide further challenges to dispersal.

The different modelling options present scientists with the opportunity to incorporate many abiotic and biotic factors, and species interactions, when modelling species distributions. Species of many taxa have been subject to modelling for a multitude of reasons. Araújo & Peterson (2012) reviewed the uses of bioclimatic envelope models incorporating all of the modelling options above. Principle among them is identifying the impact of climate change on species distributions and phylogeny, and the assessment of threat related to invasive species and disease. Others include palaeobiology, and the discovery of new populations. The diversity of application is matched by the diversity of taxa that those models have been applied to. The impact of climate change on plants (Midgley & Thuiller, 2011; Engler *et al.*, 2009; Thuiller *et al.*, 2006a; Iverson & Prasad, 1998), mammals (Warren *et al.*, 2014; Levinsky *et al.*, 2007; Thuiller *et al.*, 2006b; Erasmus *et al.*, 2002), birds (Araújo *et al.*, 2005; Erasmus *et al.*, 2002), amphibians (Araújo *et al.*, 2006), insects (Erasmus *et al.*, 2002), reptiles (Araújo *et al.*, 2006; Erasmus *et al.*, 2002), butterflies (Beaumont & Hughes, 2002), and parasites (Rödder *et al.*, 2010) have all been the subject of modelling studies.

The use of SDMs and CEMs to predict the future distributions of species is not universally accepted (Gould *et al.*, 2014; Howard *et al.*, 2014; Fordham *et al.*, 2012; Dormann, 2007; Elith *et al.*, 2006). Criticisms have been broadly grouped as: (a) that models are based on implausible assumptions and do not acknowledge, nor account for, uncertainty in the models and projections; and (b) that model based projections are contradicted by empirical evidence. Expectedly, the users of modelling techniques counter these and other criticisms (see Araújo & Peterson, 2012), and methodology continues to evolve (Gould, *et al*., 2014; Howard, *et al*., 2014). A commonly cited implausible assumption is that species distributions are determined by climate, where some suggest there is little evidence for or against it. However, the counter argument is that substantial evidence exists that climate does govern species distributions, and where climate is found not to, the shortcoming may be related to the variables selected, the scale assessed, or incomplete distribution data (Araújo & Peterson, 2012). Some of the other criticisms are statistical in nature but can be applied to many statistical techniques, for example, suitable variable selection, addressing multicollinearity, and selecting a valid modelling technique (e.g. linear versus non-linear) (Dormann, 2007). Such concerns should be addressed at a more fundamental level. Proposed guidelines for appropriate use combat each of the criticisms and should be followed if the models are to be embraced and utilized (Peterson, 2011; Franklin, 2009). However, the limitations and usefulness of the modelling options rely upon their appropriate selection and use (Araújo & Peterson, 2012), and users should acknowledge and

communicate the limitations of the methods they apply. So far, SDMs are continuing their evolution and remain a widely used methodology for investigating species distributions under the influence of climate change.

Africa's antelope species as a model system

This project studies the impact of CC on the distribution and conservation status of the 70+ species of antelopes found in Africa and the African buffalo (*Syncerus caffer*). Most of the world's antelope species are native to Africa (73 of 90 species listed by the IUCN; IUCN, 2014a); they provide an ideal study group as they are biologically diverse, and thus present an opportunity to reveal more general patterns of the effect of CC across other taxa. Various threats are causing the decline in 63% of antelope species populations in Africa with 23% being classified as threatened (IUCN, 2014a). The threats include habitat loss and agricultural encroachment linked with disease, over-exploitation through hunting, and climate change (largely related to drought and habitat-loss caused by desertification and applied to arid adapted species). Africa's economic and agricultural frailties, when linked with an increasing human population, will likely have a secondary impact, that of further habitat loss (Seto *et al.*, 2012) and exploitation of bushmeat (Lindsey *et al.*, 2013; Shackleton & Gumbo, 2010; Boko *et al.*, 2007). While the exploitation of bushmeat affects a wide number of species, it is the antelope populations that are primarily targeted (Fa & Brown, 2009; Fusari & Carpento, 2006; Brashares *et al.*, 2004). With multiple threats it is therefore important to assess how antelope species may respond to CC given our knowledge of these and other species. Africa's antelopes are also vital to the survival of many protected areas that are funded by tourism. International tourists visit protected areas primarily to see mega-herbivores (elephants, rhinos, and buffalo), and large carnivores (lions, leopards, and hyaena) (Lindsey *et al.*, 2007) whose main source of prey is antelopes (Owen-Smith & Mills, 2008). Therefore maintaining intact guilds and species diversity has been promoted for protected areas (Lindsey, *et al*., 2007).

Potential responses to climate change

The threat posed by CC requires that species respond in some way. Responses may be (a) spatial in nature, where species disperse to more favourable conditions and habitat; (b) temporal changes altering life history traits (phenology); (c) evolutionary changes over a number of generations; or (d) extinction (Bellard *et al.*, 2012; Dawson *et al.*, 2011).

There is growing evidence that range shifts are occurring and that species distributions are changing in response to climate change across a wide range of taxa (Lenoir & Svenning, 2013;

Cahill *et al.*, 2012; Hickling *et al.*, 2006; Parmesan, 2006). Hickling, *et al.* (2006) demonstrate latitudinal and elevational shifts across 16 taxonomic groups including mammals (329 species) with dispersal resulting in both expansion and contraction of ranges (Thomas *et al.*, 2006). Therefore, it may be that the dispersal ability of antelopes will be the key to understanding their response to CC, future distribution, and conservation. Antelopes, being highly mobile, are expected to disperse in response to climate change, tracking the optimal environmental conditions (see artiodactyla: Schloss, *et al*., 2012). Blue wildebeest (*Connochaetes taurinus*) and Thomson's gazelles (*Gazella thomsonii*) famously perform an annual migration driven by rainfall (Holdo *et al.*, 2009). While this is a circular migration, it demonstrates the mobile nature of antelope species. However, a permanent distribution shift would likely involve natal dispersal and the gradual incorporation of areas within suitable environmental conditions (Schloss, *et al*., 2012). There is also the possibility for dispersal to be elevational in nature where species are forced higher (Dawson *et al.*, 2011; Hickling *et al.*, 2006; Parmesan, 2006). This might affect those antelope species currently at high elevations, such as the mountain nyala (*Tragelaphus buxtoni*). However, there are also barriers to dispersal that must be considered, such as urbanized areas and unfavourable habitat.

Variation in phenology in response to CC has been shown in flowering and fruiting (plants), calling (frogs), metamorphosis (butterflies), reproduction and migration (birds) (Parmesan, 2006; Root *et al.*, 2003). Such temporal shifts need not be related to annual events; small-scale shifts could also occur whereby daily routines alter to reduce impacts from climatic change. Most antelope species are predominantly active during the early and late evening (Estes, 1991). They could, therefore, alter their active times to become more active at night and ruminate more during the day. Changes to more nocturnal activity has been seen in antelope species reacting to competition of resources (Valeix *et al.*, 2007), but whether this pattern will be replicated due to climate is unclear. Increased predator activity at night may limit this as an option. There are, however, fewer studies on mammals than other taxa (see Moyes *et al*., 2011; Root *et al.,* 2003 supplementary data), and fewer still on larger mammals. Red deer (*Cervus elaphus*) are an exception having been extensively studied over 28 years. They have displayed significant changes to reproductive phenological traits (oestrus dates, rut period, antler cast dates) linked with plant phenology (Moyes *et al.*, 2011; Langvatn & Albon, 1986). African antelope behaviour has been extensively studied in the past, but without a focus on climate change. However, there are studies on related species that may provide clues as to possible responses in the future. For example, the Arabian oryx (*Oryx*

leucoryx) demonstrated both reduced foraging, and reproductive rates in drought conditions (Ismail *et al.*, 2011). How such a response would impact a species longer term would need further consideration as fitness and populations would be affected.

Genetic adaptation is poorly understood in terms of responding to climate change (Pearson *et al.*, 2014), particularly for wild populations. Laboratory experiments on fungi species (*Saccharomyces cerevisiae*) have demonstrated rapid evolution (within 25 generations) to environmental change (Bell & Gonzalez, 2009). However, laboratory studies on fruit flies (*Drosophila birchiithese*) demonstrated that, while larger population sizes persist longer, they fail to show an evolutionary response over 10 generations (Willi & Hoffmann, 2009). Both experiments were performed under constant conditions, without environmental stochasticity, and required hundreds of individuals in the founding population. Antelopes in the wild do not have stable conditions and face many additional selective pressures and threats. Furthermore, the level of genetic variation within a population will affect its ability to adapt (Hoffman & Sgrò, 2011), but in general, species with longer generation times are at greater risk as they have fewer generations to demonstrate an evolutionary response (Jump & Peñuelas, 2005). Antelope species first reproduce between one and four years of age depending on size (van Sickle, 1990), and generation times are between five and nine years (IUCN, 2014a). This suggests that evolutionary adaptation to climate change by antelopes will be negligible before the end of the century.

Evidence of extinction caused directly by CC is also poorly understood. Cahill, *et al*. (2012) reviewed the causes of 136 localized extinctions related to CC. The proximate cause for the extinctions could be found in only seven of those. Species interactions, particularly reduction in food availability, were the most common cause of extinction rather than direct physiological tolerances. Twenty global extinctions with links to climate change are documented by the IUCN (see supplementary data from Cahill, *et al*., 2012). In all cases the cause of extinction was not solely climate change. Links to other threats such as non-climate change related habitat loss, disease, hybridization, and introduced species were contributing factors. However, climate change was linked directly to some of these threats, particularly habitat loss through drought and storms, and disease in the case of chytrid fungus.

Additional threats to antelope populations

Climate change is not the only threat facing Africa's antelopes. The IUCN groups threats into 12 categories, of which CC is one. Other categories include natural threats such as geological events, but largely consist of human threats such as over exploitation (grouped as "Biological

resource use"), pollution, human land use changes, and agriculture. These 12 categories are further subdivided into subcategories and threats. All of Africa's 19 currently threatened antelopes (categorized as vulnerable to extinct in the wild) are threatened by habitat loss (largely due to agriculture, competition with livestock, and forest removal) and exploitation (poaching, trophy hunting, pet trade, and private collections). Other threats include CC, civil and military conflict, particularly in Somalia, and harassment by domestic dogs (IUCN, 2014a). A further six species, categorized as near threatened, also list exploitation and habitat loss amongst other threats.

The threats to antelopes from over exploitation and habitat loss are likely to increase as Africa's human population is predicted to quadruple to over four billion by 2100 (United Nations, 2013). While it is difficult to predict how civil and military conflict will unfold over the coming century, the threat from CC is expected to continue and impact many species (MEA, 2005). This highlights the urgent need to identify species of conservation concern and develop plans for their protection where required.

Options for biodiversity conservation

In the past few decades governments and societies have increased their awareness of the threats facing global biodiversity, and recognized the need to protect these valuable resources. Protected areas (PAs) are the most important tool used by conservation practitioners in the conservation of biodiversity (Dudley *et al.*, 2014; Rodrigues *et al.*, 2003). PAs seek to conserve nature and their associated ecosystems. Some PAs also strive to integrate and preserve cultural values and landmarks associated with those areas. Since the formation of the first national park in 1872 (Yellowstone national park) a global network of PAs has developed that now covers 12.7% of the Earth's land mass (Dudley, *et al*., 2014). At first, most PAs were established in the developed countries and neglected much of the most biologically rich areas. However, since the 1970s a rapid increase in the allocation of PAs has taken place with half of the existing protected area network being formed in this period. This has coincided with a shift that acknowledges and focuses protection on the biologically important areas. This stems from greater global awareness of biodiversity and the threats it faces, and the foundation of conservation organizations such as the International Union for the Conservation of Nature (IUCN) in 1948. In addition, international conventions such as the Convention on Biological Diversity (CBD), formed in 1992, have been agreed and signed by the majority of the world's countries (CBD, 2015). The CBD's main aims are to conserve and promote sustainable use of biodiversity via a strategic plan consisting of 20 biodiversity

targets termed the 'Aichi Biodiversity Targets' (CBD, 2015). The CBD's current Aichi 2010 targets prescribe at least 10% of the marine and coastal areas, and 17% of land area be protected by 2020. While this is a global target, each nation is responsible for ensuring the protection of at least 10% of each of the ecoregions represented within its borders. There is also clear direction on the need to increase PAs in high biodiversity areas (CBD, 2012).

Other conventions seek to target climate change directly such as United Nations Framework Convention on Climate Change (UNFCCC) and the accompanying Kyoto Protocol. Amongst the objectives of the UNFCCC is the aim to mitigate climate change by way of reducing emissions, forest degradation, and sustainable forest management (UNFCCC, 2013). While not directly linked to biodiversity conservation, here the UNFCCC and CBD objectives start to overlap. Other integral intergovernmental organizations linked to the CBD and UNFCCC (e.g. Intergovernmental Panel on Climate Change (IPCC), European Environment Agency (EEA), and the United Nations Environment Programme (UNEP)) have been formed through other international conventions. Alongside these international organizations there are many non-governmental organizations (NGOs) and charities that contribute to the conservation of biodiversity through promoting solutions to conservation issues, providing funds for specific projects, and establishing PAs (e.g. World Wildlife Fund, Conservation International, Nature Conservancy, and World Conservation Society).

The protection of biodiversity through PAs requires careful conservation planning. Conservation planning has been defined as "the process of locating, configuring, implementing and maintaining areas that are managed to promote the persistence of biodiversity and other natural values" (Pressey *et al.*, 2007). From a global perspective, conservation planning needs to maximize the protection of biodiversity while acknowledging irreplaceability and vulnerability of an area or species. Irreplaceability of an area signifies the extent to which the loss of that area impacts on conservation objectives (i.e. if a species is only found in one area, that area has high irreplaceability compared to areas containing common species). Vulnerability of an area is the risk of that area being "transformed by extractive uses" (Margules & Pressey, 2000). Areas that are scored highly as irreplaceable and vulnerable are therefore considered priorities for conservation. This methodology can be applied to individual species, habitats, and ecosystems. Other measures of identifying conservation priorities rely on similar methods and have been applied at a global scale such as the identification of global hotspots (Myers *et al.*, 2000) and endemic bird areas (Stattersfield *et al.*, 1998). Different approaches, such as mapping the human footprint

(Sanderson *et al.*, 2002), also seek to identify areas of global importance. Brooks *et al*. (2006) found general consensus that alongside Mediterranean areas the tropics, where most antelopes are found, were of great conservation importance, irrespective of the methods used.

Tools have evolved to enable conservationists to take a systematic approach to conservation planning at global and regional scales. At a global scale, irreplaceability and vulnerability of areas is typically assessed at a coarse-resolution, but serves to direct the conservation efforts to priority hotspots. However, there is a risk that working at a coarse resolution may mean fine-scale priorities are missed or overlooked (Ferrier, 2002). Gap analysis is part of a conservation toolset that can be used to find areas which are of importance in the protection of species, i.e. "gaps in protection of biodiversity" (Scott *et al.*, 1993). Developed in conjunction with geographic information systems (GIS), gap analysis can be used at global, regional, or local scale. It is therefore useful for identifying areas of global importance, but equally at national or local levels when planning to meet conservation objectives such as the Aichi targets. Gap analysis provides details of species and areas of importance. However, in a world of finite resources, allocation of those resources for PAs must be carefully considered. To aid the design of protected area networks, conservation planning software has been developed that integrates gap analysis with details of the existing protected area network, land ownership data, the costs of protection in different areas (land purchase, accessibility costs, infrastructure, etc.), and the available funds for developing the protected area network. Using rule-based methodology, the conservation planning software then produces protected area network solutions that will provide the required level of protection within the budget allocated, or as close as possible given the resources. Additional rules, such as encouraging larger or more fragmented protected area networks can also be applied depending on requirements (Ball *et al.*, 2009). The solution provided is therefore a protected area network that expands on the existing network. Gap analysis and conservation planning software has been used to identify and plan protected area networks based on current species distributions (Delavenne *et al.*, 2012). However, they are equally able to provide solutions based on projected species distributions for the future (Carvalho *et al.*, 2011; Game *et al.*, 2011).

Having identified areas or species of importance for conservation, PAs are required in order to implement their protection. The management and ownership of PAs varies, as does the level of protection provided to the species found within them. This may be by design, for

example, the IUCN has seven management categories that range from strict protection and little human use (categories Ia and Ib) to areas managed for sustainable use of the resources within (category VI) (see Lockwood, 2006). However, many other protected areas have been labelled "paper parks" that have little management and largely fail to protect biodiversity which should be their main aim (Bonham *et al.*, 2008). Privately protected areas have been identified as being "an essential component in achieving the CBD Aichi Biodiversity Target" (Stolton *et al.*, 2014). However, while some countries' privately protected areas are integrated as part of their national conservation strategies (e.g. South Africa and Kenya), in other countries they are not. Some privately protected areas are criticized for their lack of clarity over their management resulting in difficulties when assessing the level of protection provided or whether they can be classified as PAs at all (Stolton *et al.*, 2014). Globally there is a recognized need to improve the performance of PAs and this is particularly the case in Africa (Leverington *et al.*, 2008). Despite the concerns over some PAs they continue to be the main mechanism of conservation for most species, including antelopes.

Recently there has been increased focus on PAs that are managed and maintained not by national or local government, nor by private companies or individuals, but by local communities. In eastern and southern Africa this shift in management was driven by the failure of conservation policies in the 1970s and 1980s (Gibson & Marks, 1995). Community protected areas rely on the community within those areas taking responsibility for some or all management, monitoring, protection, and sustainable harvesting of the resources therein. The communities then benefit from development and financing from ecotourism, hunting, and/or the services they provide. Studies show that where community management is in place the degradation of those areas is typically reduced and less variable than conventionally managed PAs (Porter-Bolland *et al.*, 2012; Ellis & Porter-Bolland, 2008).

Ex-situ conservation and reintroductions

Beyond *in-situ* protection, species are also found in conservation centres, such as zoos and aquariums. In these centres, populations are managed and maintained primarily for conservation purposes. Amongst the goals of zoos and aquariums is to breed, translocate, and re-introduce animals (Penning *et al.*, 2009). Via these goals they can have, and have had, direct input into the conservation of many species including antelopes in Africa. Probably the highest profile reintroduction of antelopes has been that of the scimitar-horned oryx (*Oryx dammah*) whose current captive population was largely formed in the 1960s (Gilbert & Woodfine, 2004). Subsequently, the species' wild population declined due to overhunting,

habitat loss, and competition with livestock until it was declared extinct in the wild in 2000 (IUCN SSC Antelope Specialist Group, 2013). Over 1,500 individuals are now globally managed in captivity, with many others found in private collections. Reintroductions into fenced areas began in 1985 prior to the declaration of extinction in the wild. To date, reintroductions have taken place in three countries (Tunisia, Morocco, and Senegal) with Niger to follow. These are ongoing efforts with all populations remaining in fenced areas for protection and management (IUCN SSC Antelope Specialist Group, 2013). Similar reintroduction projects are ongoing for the critically endangered addax (*Addax nasomaculatus*) using the same protected areas as the scimitar-horned oryx in Tunisia (Bou Hedma national park) and Morocco (Soussa-Massa national park) (Newby & Wacher, 2008). Such long-term efforts provide evidence of sustained will to conserve antelope species in Africa.

Reintroductions need not rely on *ex-situ* populations as seen with scimitar-horned oryx and addax. Former populations have been re-established using wild individuals (Clegg *et al.*, 2013) with these translocations generally being more successful than those using captive animals (Fisher & Lindenmayer, 2000; Bright & Morris, 1994). All translocations bring with them risks that must be recognized, assessed, and avoided or mitigated where possible. The risks include: the introduction of disease or invasive species; ecological impacts at multiple levels from species to ecosystem function; negative affect on the source population through the removal of individuals; socio-economic impacts including possible danger to humans from the reintroduced species; and financial risks of damage caused by the introduced species, such as foraging on local crops (IUCN/SSC, 2013). These risks may be reduced if a species is being reintroduced into an indigenous or historic area where the species has been previously lost. In this case the aim is to re-establish the natural ecosystem and equilibrium therein. However, where species are introduced to non-indigenous areas the risks must be very carefully considered. This can be the case when mitigation translocations take place in response to anthropogenic caused habitat loss.

The use of mitigation translocations is increasing (IUCN/SSC, 2013), but is not commonly referenced in relation to CC despite arguably being anthropogenic habitat loss. Translocation of animals due to CC may be necessary where, (a) a species is unable to disperse naturally due to lack of interconnecting habitat and habitat corridors are not viable; or (b) the species is unable to disperse rapidly enough to track the climatic change (Hulme, 2005). Where climate driven translocations are required, new areas need to be identified. The IUCN

guidelines recommend that those areas be historically indigenous and climatically suitable for the "foreseeable future" (IUCN/SSC, 2013). However, given that a species' range is broadly based on its climatic envelope, there may be no climatically suitable area within indigenous areas that remain climatically suitable for the foreseeable future. Therefore, assuming that climate suitability is paramount to the survival of a species, areas beyond a species' historic indigenous range may have to be considered, although this results in the translocation being classified as an assisted colonization and is considered less desirable (IUCN/SSC, 2013).

While the risks associated with translocations are considerable, reintroductions have been successful in the past and are a viable option for the protection of species. Owen-Smith (2003) found that 85% (17 of 20) of ungulate based translocations had been successful. Success can be improved by using wild individuals (Fisher & Lindenmayer, 2000; Bright & Morris, 1994), a larger founding population (Hulme 2005; Fisher & Lindenmayer, 2000; Wolf, *et al*., 1998), timing the release to coordinate with seasonal food availability (Bright & Morris, 1994), and ensuring better habitat quality (Wolf *et al.*, 1998). An area with suitable climate is fundamental to species survival and therefore if all of these important components are in place, the likelihood of project success should increase. This process begins with the fundamental issue of identifying areas of climatic suitability. These areas would then be assessed for habitat suitability before the further factors can be addressed and project plans developed. This must all be coordinated with the impact and risk assessments for the other resident species before implementation. This thesis addresses the first part of this process by identifying climatically suitable areas for Africa's antelope species which are threatened by climate change. I also identify which areas will potentially reduce competition from other antelope species and limit the number of novel antelope species encountered.

Thus, the general aim of this thesis is to assess the impact of climate change on the distribution and conservation status of Africa's antelope species using species distribution modelling and ensemble predictions. I present options for the protection of all antelope species through a continent-wide protected area network. I also provide recommendations for translocation options for species directly threatened by climate change or lack of existing protection. Following a project methodology chapter, I present four data chapters (chapters three to six), summarized below, each with individual aims as part of a cohesive analysis of antelope threats and conservation opportunities throughout the 21st century.

Chapter three develops the species distribution models used to predict antelope distributions throughout this thesis. The biotic and abiotic variables relevant to determine species distributions are identified and an analysis of the performance of the resulting models is presented. These models are used to identify each species' optimal climatic conditions. Accounting for phylogeny, I then investigate relationships between species trait data (morphological, ecological, behavioural, and range size) and the optimal climatic conditions of species. This chapter also investigates the relationship between antelope species richness and precipitation.

Chapter four uses the models developed in data chapter one to predict the distribution of Africa's antelopes in 2080. Using three climate scenarios (A1B, A2, and B1), and ensemble models that incorporate climate predictions from three climate models, suitable climatic condition predictions are made for each species, for 2030, 2055, and 2080. Three modelling approaches are presented that offer different views of the future. The first two incorporate contrasting species dispersal options where species are either unable to disperse from their current range or can disperse at a given velocity based on body mass. The final approach identifies all climatically suitable areas which are connected to the species' current range through time. The models are refined to also incorporate a habitat filter that restricts dispersal of specialist species through unfavourable habitat. The analysis assesses the impact of climate change on the range size of species, and investigates relationships between the change in range and species trait data.

Chapter five uses the species distribution predictions developed for data chapter two (A1B climate scenario) to develop options for a continent-wide protected area network based on the existing IUCN network. This incorporates two different levels of protection for species providing low and high protection options. Each species is assessed for PA coverage based on IUCN PAs and non-IUCN PAs. Three countries (Kenya, Namibia, and Tanzania) are considered individually to assess the contribution of community led conservation. Community led conservation areas are a subset of Africa's non-IUCN PAs and, for these three countries, are compared to IUCN PAs as well as the remaining non-IUCN PAs. I review areas that are highlighted as important for expansion of the protected area network, and consider how different changes in range (contraction, expansion, or shifts) relate to PA coverage.

Chapter six identifies species that are at special risk either due to climate change or because they are offered no protection by the existing IUCN protected area network. I look at the options for those species including the potential suitability of translocation beyond their

indigenous range. For all species, the aim is to identify areas (a) that are climatically suitable; (b) where they would encounter relatively few novel species; and (c) where the niche overlap with other antelopes is relatively low. This acts as a first step in identifying areas should translocation be necessary. I also consider the need for new terminology to denote areas that are predicted to become indigenous if the species were free to disperse naturally in the absence of conservation threats. Currently, translocations to these areas would be categorized as an assisted colonization because existing guidelines focus on a species' historic or present indigenous distribution rather than its future potential.

Finally, I provide a synthesis of the work contained within this thesis. This places the findings in context and outlines the importance of studies such as these. Here I also review the limitations of the study, potential for improvements, and possible future directions for species distribution modelling and conservation planning based on their predictions.

2. Project methodology

Due to the reuse of similar methodology in multiple data chapters, below I detail the common methodological approaches used in this project. All statistics and results were produced using R version 2.15.2 (R Core Team , 2012). Any additional R packages are acknowledged in the relevant sections or below.

2.1 Rasterization of ESRI shapefiles

The species distribution maps were extracted from the IUCN distribution maps (IUCN, 2011). The distribution data provides presence/absence data for the species in those areas. The distribution maps, provided as ESRI shapefiles (ESRI, 2011), were rasterized to the 10' (arcminutes) grid resolution used throughout this project. This process involved Python coding and Java programs to correctly identify the 10' grid squares that overlapped the shape files. The following procedure enabled rasterization:

1. Export the species distribution shapefiles to comma delimited files from ArcGIS (ESRI, 2011) using Python code.
2. Import into Microsoft Access.
3. Convert the shape file to raster format via central point determinacy as follows. For each 10' grid cell the central point is taken and a virtual line is drawn along that longitude eastwards to the end of the grid. Each time that line crosses a border of the species' range it is recorded. If, when reaching the grid edge, an odd number of borders has been crossed then the original grid cell is considered within the species' range. If not (even), it is considered outside the species' range (see Figure 2-1).

The IUCN data provides the species distribution with a number of levels of confidence. For this project the highest level of confidence is being used, that of 'Extant' and not including 'Probably Extant' or 'Possibly Extant' (IUCN,2010b). In addition, only areas considered as 'Native' are being analysed after it was found species classified as 'reintroduced' had been introduced outside of their natural range (Scimitar-horned oryx).

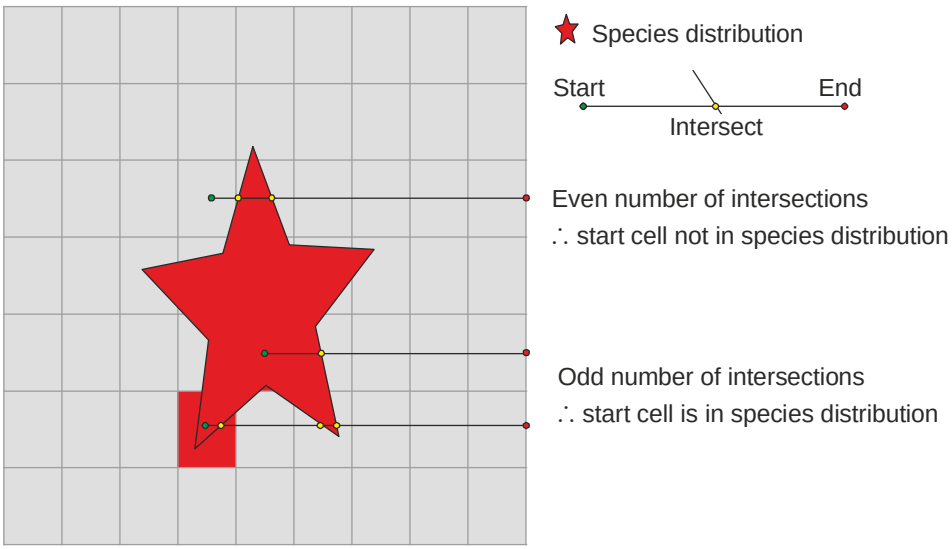

Figure 2-1: Rasterization of ESRI shapefile using central point determinacy. A horizontal line is drawn from the centre of each cell. If there are an odd number of intersections with a shapefile's border the cell is found to be within the shapefile.

2.2 R & BIOMOD

The statistical modelling of species distributions for this project uses R (R Core Team , 2012) and the package BIOMOD (Thuiller *et al.*, 2009). BIOMOD allows the use of multiple modelling methods including generalized linear models (GLM), generalized additive models (GAM), surface range envelopes (SRE), random forests (RF), multivariate adaptive regression splines (MARS), classification tree analysis (CTA), mixture discriminate analysis (MDA), and artificial neural networks (ANN) (Thuiller *et al.*, 2009). All of these modelling methods can be used to model species distributions with varying level of performance measured by computing the area under the curve (AUC) plot (Marmion *et al.*, 2009; Huntley *et al.*, 2004) or Kappa coefficient (Thuiller *et al.*, 2009; Randin *et al.*, 2006). GLMs and GAMs have a strong statistical foundation and are known to "realistically model ecological relationships" (Elith *et al.*, 2006). GLM and GAM also produce more reliable modelling when those models will be used to predict distributions over different time periods. This is due to the curved nature of the models which makes them able to accommodate values beyond those used to build the model (extrapolation modelling) (Marmion *et al.*, 2009). RF would not function due to the size of the dataset, however, Marmion *et al.* note that RF performs well for interpolation modelling (where all future values are bound by the values used to build the model) but not extrapolation as required for this project. Marmion *et al.*'s review also states that ANN and MDA suffer from producing very complex models as they do not selectively pick the

significant variables. SRE, MARS and CTA produced poorer fitting models than GLM and GAM during testing.

Both GLM and GAM modelling within BIOMOD were considered after removing the other modelling options. GLM, including quadratic functions, was selected because it provides good performance (Elith, *et al*., 2006) and does not suffer from overfitting, as is possible with GAM, which may reduce transferability; i.e. where models are applied to different geographic areas or temporal periods (Randin, *et al.*, 2006; Austin, 2002). Overfitting occurs when GAM, using smoothing splines, can produce a model that fits the data very closely, but not the wider ecological or bioclimatic envelope. For example, Figure 2-2 shows a GAM and GLM (quadratic function) modelling the probability of a species being located in an area against the coldest mean temperature. The GAM graph suggests the species is less likely to be present at 7° than 6° or 9°. This may fit the data, but adds little to our ecological understanding of the species.

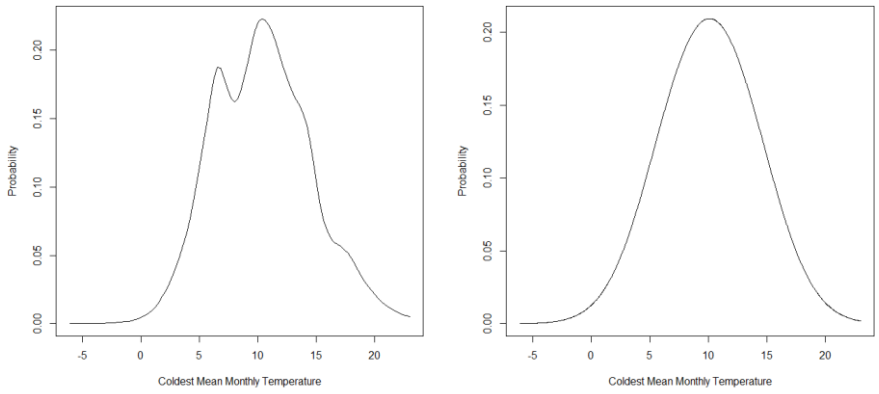

Figure 2-2: Left: Overfitting in GAM using seven smoothing terms. Due to smoothing it is possible that the model will fit the data but may not make ecological sense. Right: A GLM fit providing a more understandable model, albeit may not fit the data as closely. Note: this is simplified data for demonstration.

The GLM models were calibrated using a random sample of data (70%) and stepwise GLM method (stepAIC) resulting in the most parsimonious model based on Akaike Information Criteria (AIC) (Thuiller *et al.*, 2003). The models are then evaluated against the remaining 30% of the data using AUC, sensitivity (true positives), and specificity (true negatives) (Swets, 1988). For each species a probability threshold (cut off) is produced maximising the percentage of correctly predicted presences and absences (Thuiller *et al.*, 2006a; Pearce & Ferrier, 2000) (see 2.3).

The models are finally used to produce optimal values for each of the climate variables for correlation with species trait data. These were produced from the model intercept and coefficients extracting the vertex values. Where the values were outside of the climatic range for Africa the relevant minimum or maximum value within Africa was used for that species. A small number of models resulted in a nadir within the range, these species were removed from the optimal value analysis. The value for optimal temperature range was produced from the subtraction of optimal maximum and optimal minimum temperatures where both values were available.

2.3 Sensitivity, specificity, and cut off in BIOMOD

Species distribution models based on GLMs were produced for all species using the R package BIOMOD (Thuiller, *et al*., 2009; see 2.2). Using the GLM model allows the prediction of whether a species will be present in any particular grid cell and the probability of that species being present. With a binomial response the probability, which ranges between 0 and 1, requires a *cut-off* value to determine a presence or absence in a cell. BIOMOD creates a cut off value between 0 and 1 by measuring the sensitivity (number of correctly predicted presences) and specificity (number of correctly predicted absences). This is achieved in the following way (note the values are multiplied by 1000 for simplicity) assuming for this species there are 103 true occurrences representing the species distribution:

1. The default cut-off is set at 0.
2. All predictions are above 0 so all 103 true occurrences are included providing 100% (1) sensitivity but no predictions are under 0 and specificity is 0% (0), the difference between them is 1 (100%-0%).
3. Next iteration cut-off is set to 0.5; the same test is applied with the same results.
4. As there is no change in the difference the process continues until the cut-off is 120 and the sensitivity and specificity change.
5. 81 predictions from 103 occurrences are above the cut-off of 120 therefore the sensitivity is 78.6%
6. 82871 predictions are below 120 from 89714 therefore specificity is 92.37%
7. Subtract 0.786 (78.6%) from 0.924 (92.37%) to get a value (0.138) this value is less than the previous difference of 1 so the process continues.
8. The next iteration cut off at 120.5.
9. The same sensitivity is recorded as the same 81 predictions are still predicted.

10. However, a better specificity is found as 84448 predictions are below 120.5 giving 94.1%
11. The difference between sensitivity and specificity is 0.155. Typically the point at which the difference starts to increase sets the cut-off point; however, it is possible for the specificity to continue to increase whilst maintaining the same sensitivity. Therefore while the sensitivity remains the same the process can continue.
12. When the cut off is 122.5 sensitivity drops to 77.7% but the specificity may still rise. However, as sensitivity has dropped this is a poorer cut-off value and therefore the cut-off is set at the previous value (122). All grid cells with a value equal or above 122 are considered to be suitable for the species.

2.4 Variable importance in BIOMOD

Selection of the model variables required ensuring as little correlation between those variables as possible and also recognizing which of the variables were most important. To do this a 'variable importance' value (BIOMOD function) was produced for each variable on each of the preliminary model production runs for each species. Variable importance values are generated using random replacement and model re-evaluation. Each of the model's variables values are scrambled in turn and the model is re-evaluated to identify the importance of each variable to the model. These values were then collated for each model production run to find which of the variables were most important for the majority of species. While these values cannot be directly compared between models due to different numbers and variables in each test, this process did provide an understanding of general importance of variables for the majority of species.

2.5 Data set and variable selection

2.5.1 Data scale

The SDMs were constructed using the independent (predictor) variables detailed below. A set of data was generated for each of the variables at the same scale. The selected scale can result in different results. This has been seen in studies in Europe where the models based on a 10' scale (approximately 18km x 18km [New *et al.*, 2002]) predict a complete loss of habitat, whereas a 25m scale predict suitable habitat for 100% of species (see Bellard, *et al.,* 2012; Randin, *et al.* 2009). Randin *et al*. (2009) used accurate climatic data and elevation, to interpolate variables at a local level (25m x 25m). It is possible to model climatic data for Africa at this scale via interpolation, but due to the limited number of weather stations in the

area this would not add additional information and would limit the validity of that data (New, *et al.*, 2002). In addition, the 10' scale has successfully been used to model mammalian species distributions for Africa previously (Thuiller, *et al.,* 2006). Therefore all other datasets were aggregated or disaggregated to this scale/domain.

2.5.2 Land transformation data

Land Transformation (LT) data (Sanderson *et al.*, 2002) was incorporated using a weighted filter. The LT dataset represents the 'Human Footprint' and uses four sources of data to demonstrate the human influence on Earth. These sources are population density, LT, access and electrical power infrastructure. LT data was aggregated (resampled) from the original 0.5' resolution to 10' scale. The maximum values were calculated for each grid cell. Values range from 0-100 (no transformation-complete transformation) and were subsequently divided by 1000 for incorporation into the distribution probabilities. The initial probability (IP) of occurrence from the model is weighted by the LT to provide a final probability (FP) for each grid cell: $FP_i = IP_i \times LT_i$ where i is a 10' grid cell (Thuiller *et al.*, 2006b).

2.5.3 Data sources

2.5.3.1 Climate variables present and future

Climate data was sourced from WorldClim (Hijmans *et al.*, 2005) and used to provide both the current and future climate conditions based on a 10' grid. This dataset provides the basic variables of mean precipitation and temperature. The CRU CL2.0 dataset (New *et al.*, 2002) provided wind, and elevation data required to produce the potential evapotranspiration values (PET) (calculations from Allen, *et al.,* 1998 [Ch. 3-4]) that have been used to predict species distributions (see - plants, insects, birds: Huntley, *et al.,* 2004*;* plants: Thuiller, *et al.*, 2005; mammals: Thuiller, *et al.*, 2006).

By using the temperature range, and grouping the monthly values in uniquely different ways, it was possible to evaluate climatic variables as below:

- Mean monthly/yearly temperature
- Hottest/coldest mean monthly temperature
- Absolute hottest/coldest monthly temperature (hottest/coldest month +/- ½ the temperature range)
- Temperature Range (absolute hottest – absolute coldest)
- Mean monthly/annual precipitation (with/without log values)
- Driest/Wettest two months
- Driest/Wettest consecutive three months (with/without log values)

- Potential (Reference) evapotranspiration (based on climate, elevation, solar radiation)

2.5.3.2 Soil and vegetation - variable aggregation

The non-climatic datasets were Normalized Difference Vegetation Index (NDVI) (Tucker *et al.*, 2005), and two soil datasets from the Harmonized World Soil Database (HWSD, 2012) and the US Department of Agriculture (USDA, 2005). These datasets were chosen because of the ecological links to antelope. NDVI data has previously been demonstrated as a good indicator of antelope distribution and abundance (Pettorelli *et al.*, 2009; Mueller *et al.*, 2007). Soil data has also been suggested as an important factor influencing species distribution (savannah herbivores: East, 1984; burrowing owls: Stevens, et al., 2012). The HWSD dataset contained a number of variables for soil including the selected *Cation Exchange Capacity* (CEC) value for topsoil. This provided the numeric nutrient fixing capacity of the soil [range 0-88.4] (Nachtergaele *et al.*, 2012). The USDA dataset offered categorical soil type data.

These variables were aggregated as their original scale was finer than the climatic data. NDVI data were at a scale of 8x8km. The two sets of soil data were on 30'' (arcseconds) scale. All datasets were aggregated to 10' scale. All aggregation was achieved using custom written Java programs that finds all the 30'' or 8x8km grid cells within each 10' grid cell. For the soil data the mode value was then used to aggregate the data providing the most common soil. For the NDVI data, the mean value was used.

2.5.3.3 Ecological and morphological data

The data on diet, morphological attributes, and social structure were collated from a number of sources (Bro-Jørgensen, 2007, 2008, unpublished; Kingdon, 2003; Gagnon & Chew, 2000; Estes, 1991; Jarman, 1974)[1]. These data are used to establish relationships

[1] All available diet proportion data are from Gagnon and Chew (2000) except hirola that was not in the dataset. Hirola (*Beatragus hunteri*) values are set as 92.5% grass, 7.5% browse, 0% fruit following Cerling et al.'s finding that C_3 vegetation formed 5-10% of the diet (Cerling *et al.*, 2003). The hirola is a member of the alcelaphini tribe of antelopes (Estes, 1991) that are considered "predominately pure grazers" (Cerling *et al.*, 2003). The other species in the tribe of a similar size have no fruit in their diet with similar amounts of browse to that set above (from Gagnon & Chew, 2000).

between behavioural, morphological, and ecological traits with range change over time, climatic conditions, conservation status, and dispersal ability.

2.5.4 Variable selection

The following describes the independent processes used to identify the variables to be included in the species distribution models:

1. BIOMOD models for all species were produced 26 times using different combinations of variables. On each occasion, the variable importance function (see 2.4) showed which variables were most important within the models. This identified the commonly important variables, across the 26 BIOMOD iterations, for multiple species. Throughout the process the sensitivity, specificity and area under the curve (AUC) values for the receiver operating characteristic (ROC) were analysed to ensure models retained "High usefulness" (AUC > 0.9) where possible (see Huntley *et al.*, 2004).
2. Variables needed to be either static, or have future projections, to allow species distributions to be predicted in the future. Soil was assumed static, as was elevation. However, vegetation indices, such as NDVI, change over time. There are no continent-wide projections for vegetation indices so these were eliminated. NDVI also had a strong correlation with mean precipitation in Africa (r = 0.83).
3. Correlated variables were identified by correlation analysis and principal components analysis (PCA). The variables analysed via PCA were a reduced set of all those evaluated via BIOMOD. I selected the most important variables from the variable importance analysis above (Hottest, coldest, mean, and range of temperature; Log of mean precipitation). Where two or more variables derived from a single variable (e.g. mean precipitation, log of mean precipitation), I selected the variable from those models producing the highest AUC scores. I included the variables that have previously been used in identifying species distributions (elevation, soil, and evapotranspiration). In the case of soil, the nutrient fixing capacity variable was used as this offered data for 100% of the study areas where the others did not. Finally, I include driest and wettest three month periods. The driest three month period variable has been proven valuable in identifying species distributions (Butt *et al.*, 2008; Bukley & Jetz, 2007). The wettest three month period is not commonly used, however, in forest areas the wettest three month period is

negatively associated with above-ground biomass (Lewis *et al.*, 2013). This has the potential to impact on those species and was therefore included in the PCA.

Due to the high level of correlation the eigenvalues were calculated for each PCA component; those with values greater than one were then further analysed (Kaiser-Guttman criterion: Foster *et al*., 2012; Jackson, 1993). Table 2-1 provides the summary of the PCA. The log of annual precipitation was consistently the most important variable (from BIOMOD) and was also highlighted in principal component 1 (PC1) in the PCA analysis. Table 2-2 displays the variable loadings (eigenvectors) for each principal component. PC1 highlights the importance of hottest temperature and temperature range alongside the log of annual precipitation. It suggests links between high rainfall and small ranges in temperature which agrees with tropical forest areas. This also suggests lower hottest temperatures in high rainfall areas which, when taking the large desert areas with low rainfall and high hottest temperatures, seems reliable.

PC2 demonstrates the importance of mean temperature, coldest temperature, and elevation. It logically suggests that higher elevation is tied to colder mean temperature and colder coldest temperatures, and *vice versa*. PC3 accounts for 10.3% of the variance and is dominated (eigenvector 0.915) by soil nutrient fixing capacity suggesting this is an important variable.

4. Two variables displaying correlation and/or similarities may have different ecological importance. For example, hottest mean temperature has a negative correlation (r = -0.57) with the annual precipitation. However, they are hypothesized to be independently important variables in relation to the ecology and morphology of some species, for example, desert species.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Standard deviation	2.063	1.651	1.014	0.898	0.750	0.586	0.390	0.329	0.137	0.000
Eigenvalues	4.257	2.724	1.027	0.806	0.562	0.343	0.152	0.109	0.019	0.000
Proportion of Variance	0.426	0.273	0.103	0.081	0.056	0.034	0.015	0.011	0.002	0.000
Cumulative Proportion	0.426	0.698	0.801	0.882	0.938	0.972	0.987	0.998	1.000	1.000

Table 2-1: Summary of principal components analysis. The first three principal components with eigenvalues greater than 1, and accounting for 80% of the variance, are further assessed (Kaiser-Guttman criterion: Foster, et al., 2012; Jackson, 1993).

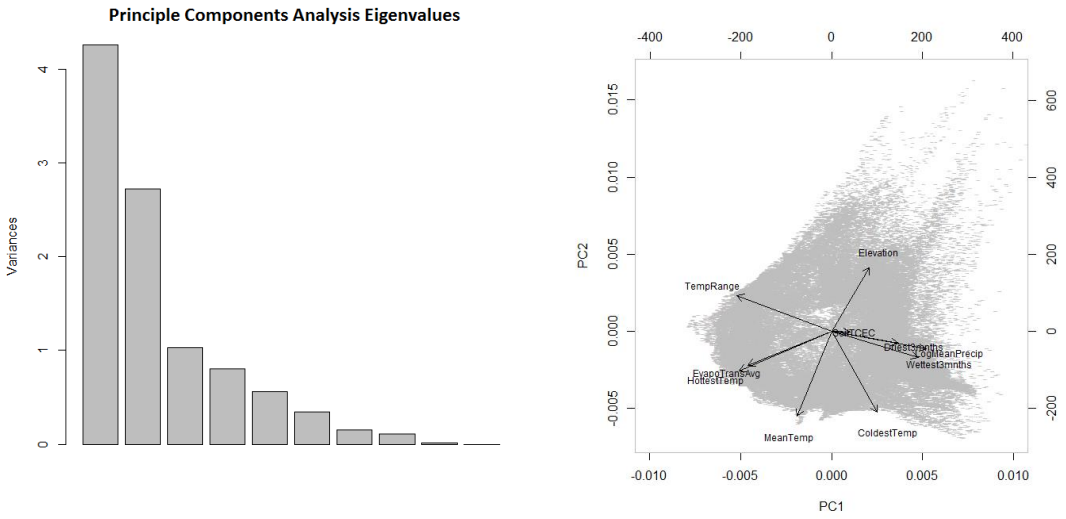

Figure 2-3: Left – Eigenvalues from the principal component analysis identifying the importance of the first two principal components. Right – a biplot of the principal components analysis demonstrating the close correlation of the precipitation variables (grouped together). Principal components axis 1 (labelled PC1) identifies the log of annual precipitation (LogMeanPrecip), hottest temperature (HottestTemp), and Temperature Range (TempRange) as important variables within that principal component (see Table 2-2 for loading scores). Principal components axis 2 (PC2) is influenced by Coldest Temperature (ColdestTemp), Mean Temperature (MeanTemp), and Elevation. The variables analysed are those often identified as important via BIOMOD's variable importance that could be projected into the future, or are static (elevation, soil nutrient fixing capacity [SoilTCEC]).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Coldest temperature	0.202	**-0.535**	0.040	0.028	-0.013	0.299	-0.035	0.280	0.462	-0.536
Hottest temperature	**-0.412**	-0.260	0.009	-0.064	-0.115	-0.398	-0.223	0.379	0.425	0.462
Temperature range	**-0.422**	0.236	-0.024	-0.063	-0.065	-0.487	-0.119	0.035	-0.073	-0.707
Mean temperature	-0.153	**-0.562**	0.019	-0.132	-0.125	0.038	-0.057	0.237	-0.753	0.000
Log driest 3 months	0.296	-0.079	-0.313	0.544	-0.659	-0.268	0.024	-0.064	-0.031	0.000
Log wettest 3 months	0.385	-0.172	0.016	-0.400	0.091	-0.532	0.607	0.016	0.038	0.000
Soil nutrient fixing capacity	0.081	-0.007	**0.915**	0.355	-0.038	-0.158	0.026	0.015	-0.049	0.000
Elevation	0.167	**0.418**	0.169	-0.445	-0.558	0.221	-0.021	0.458	-0.014	0.000
Log mean precipitation	**0.421**	-0.117	0.080	-0.341	-0.015	-0.229	-0.716	-0.348	-0.001	0.000
Evapo-transpiration	-0.374	-0.224	0.164	-0.276	-0.460	0.180	0.220	-0.621	0.169	0.000

Table 2-2: Principal components loadings for each variable within the principal component. PC1-3 are those where the eigenvalues are greater than 1 and are investigated further. Bold values are significant variables within the principal components.

2.5.5 Final model variables

Models including fewer variables were preferred for both model parsimony and to provide clarity in the production of the optimal climatic values for species. Following the PCA and variable importance assessment the three following variables were selected:

- Log of annual precipitation: This was consistently the most important variable for a wide range of species. PCA confirmed this importance linked with temperature variables. Rainfall has previously been highlighted as an important variable in predicting savannah species and biomass (Hopcraft *et al.*, 2009; East, 1984). Rainfall is also a key driver of vegetation in an area which in turn provides different foraging opportunities for species.
- Hottest temperature: Highlighted by PC1 as important and as a physiologically important variable. Each species has a thermoneutral zone, a range of conditions where a species can be active without the body temperature exceeding high or low limits, beyond which they must expend energy and/or water to maintain body temperatures within tolerance levels. Larger species typically have wider thermoneutral zones due to smaller body surface to mass ratio and reduced thermal conductance (Owen-Smith, 2002; Schmidt-Nielsen, 1990; Lindstedt & Boyce, 1985). Hottest temperature is closely correlated with temperature range and important in the production of optimal temperature range for each species.
- Coldest temperature: This variable was highlighted in PC2 and is important in relation to the thermoneutral zones and the production of the optimal temperature ranges.

As noted above, hottest and coldest temperatures were selected as they offered the opportunity to produce the temperature range optimal value for each species. Temperature range itself was not included in the model as it was originally derived from hottest and coldest temperatures and was strongly correlated with both. Hottest and coldest temperatures were also constantly high in the variable importance scores. These temperature variables provide the opportunity to investigate biome specific traits such as desert (large temperature ranges), and tropical forest (small temperature ranges). These final three variables offer models with similarly high sensitivity, specificity, and AUC values compared to models with more variables.

Other variables highlighted as important, but not included in the models, were soil nutrient fixing capacity, mean temperature and range, and elevation. The USDA soil dataset only

covers 90% of Africa and for this reason it was not included in the model. Soil variables were also consistently very low on the variable importance results from BIOMOD. Mean temperature and range are strongly correlated to both hottest and coldest temperatures. Elevation is strongly negatively correlated with hottest temperature (Pearson's product-moment correlation: $r = -0.607$; $p<0.001$).

2.6 Comparative analysis with phylogenetic control

In the past phylogenetic relationships were largely ignored, but recently there is growing acceptance that phylogenetic signal be assessed, and accounted for, in the presentation of results (Freckleton & Harvey, 2006; Freckleton *et al.*, 2003). Closely related species with similar evolutionary histories will likely occupy similar ecological niches thus threatening statistical independence. Antelopes are grouped in distinct tribes with similar morphological features. There are a number of groups and species that have shared evolutionary and speciation events through history. For this reason all behavioural, ecological, and morphological analyses were conducted with and without control for phylogeny to correct for non-independence of data (Martins & Hansen, 1997). Fernández and Vrba's (2005) phylogenetic tree was selected as it provides a detailed compilation of phylogenetic work dedicated to all ruminants, including antelopes and the African buffalo. This was preferred over the commonly used supertree developed by Bininda-Emonds *et al.* (2007) which had a broad mammal focus. Upon review of both trees at the antelope level, it was clear that finer resolution is provided by the Fernández and Vrba tree (See Figure 2-4). Fernández and Vrba's (2005) tree is also a focused study on the taxa in question whereas the Bininda-Emonds *et al's* (2007) tree was not, nor was it clear from where the data, for the antelope taxa, derived.

The R package 'geiger' fitContinuous function (Harmon *et al.*, 2015) was used to determine which (if any) evolutionary model best described the evolution for each species trait (English *et al.*, 2012; Walls, 2011). Akaike's information criteria (AIC) was used to select the best fitting model (Table 2-3). Each of those evolutionary models was then integrated into a model to investigate the relationship between the trait and the optimum climatic conditions for species. In addition multivariate models were produced to find the traits that predict optimal climatic conditions. Finally, multivariate models to predict diet diversity and global range size using climatic, dietary, and mass of the species as explanatory variables were produced. The models were produced using linear and quadratic functions in 'gls' (Brownian

and Ornstein-Uhlenbeck [OU] evolutionary models, 'geiger' package) and Phylogenetic Generalised Least Squares 'pgls' (lambda, kappa, and delta evolutionary models, 'caper' R package using maximum likelihood). Where branch lengths were 0 reflecting polytomies, these were reset to 0.0001 to enable pgls to perform comparisons following Symonds & Tattersall (2010). Using pgls, a maximum likelihood (ML) process obtains a value for lambda, kappa, and delta for the related variables (Table 2-3). The selected evolutionary models for fruit percentage and global range were Brownian and White respectively. To produce a Brownian motion evolutionary model the maximum likelihood values are set at λ=1 (Pagel, 1999). To produce the white noise evolutionary model, λ was set to 0.

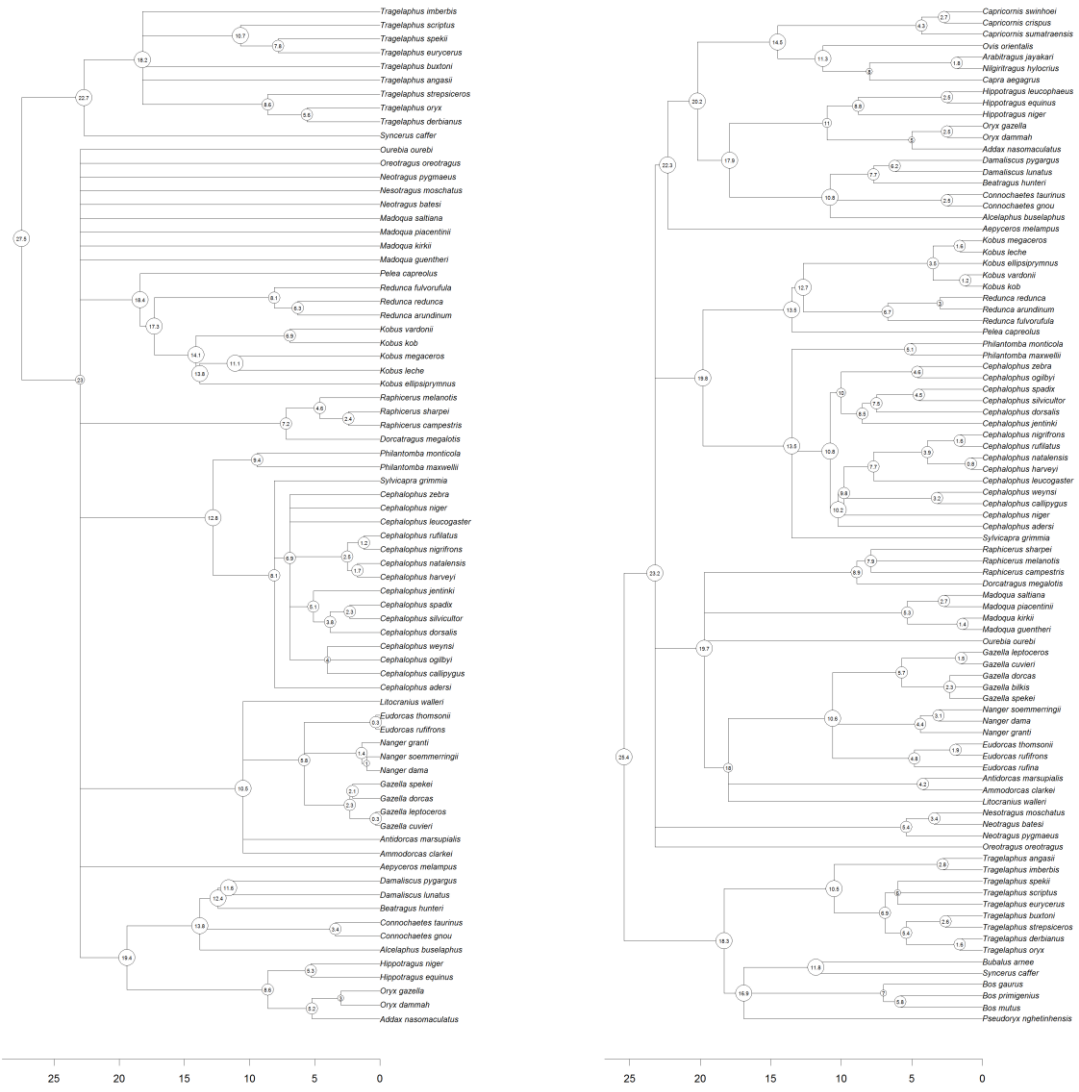

Figure 2-4: Comparison of phylogenetic trees for the species considered in this thesis. Left: Extracted from Bininda-Emonds et al. (2007) supertree. Right: Extracted from Fernández & Vrba (2005) tree of extant bovids.

Evolutionary models

The evolutionary models considered above each differ from the "Brownian motion" model of trait evolution which predicts that closer related species are more similar to each other. This relies on the assumptions that traits evolve at a linear rate in time without an end or optimal point, and that they evolve independently so multiple species can evolve similar traits (Freckleton & Harvey, 2006). These assumptions are restrictive and therefore many alternatives/modifications have been produced. The similarity between closely related species due to common descent is labelled "phylogenetic signal".

	Evolutionary model							Selection of model	
Trait	Brownian	Lambda	Delta	Kappa	OU	EB	White	Min AIC	Selected model
Adult Mass	150.90	152.90	146.14	152.90	152.90	NA	251.45	146.14	Delta
Group Size	172.89	170.24	173.51	167.27	172.97	174.89	220.06	167.27	Kappa
Global Range	359.41	315.82	340.54	349.60	315.82	361.41	313.82	313.82	White
Grass % in Diet	669.21	651.62	656.39	671.21	644.89	671.21	1385.33	644.89	OU
Browse % in Diet	658.36	638.81	643.00	660.36	639.00	660.36	1035.02	638.81	Lambda
Fruit % in Diet	572.32	574.32	573.15	573.94	574.32	NA	1146.35	572.32	Brownian
Diet Diversity	-36.21	-46.42	-39.79	-39.03	-40.61	-34.21	-14.87	-46.42	Lambda
Horn/Shoulder Index	-72.42	-72.30	-70.43	-72.49	-70.45	NA	-4.69	-72.49	Kappa
Optimal Hottest Temperature	425.40	384.80	407.23	403.07	384.76	427.40	382.80	382.80	White
Optimal Coldest Temperature	399.20	377.70	386.94	392.77	381.65	401.20	381.43	377.70	Lambda
Temperature Range	329.33	314.46	319.84	321.87	316.93	331.33	318.74	314.46	Lambda
Optimal Annual Precipitation	-34.54	-52.77	-43.69	-53.80	-45.74	-32.54	-25.74	-53.80	Kappa

Table 2-3: Analysis of evolutionary models. Values are AIC results. OU = Ornstein-Uhlenbeck; EB = Early Burst; White = white noise (no phylogenetic signal). EB values of NA are default values where the value could not be calculated.

Pagel (1999) provides three of the evolutionary models: Lambda (λ), Kappa (κ) and Delta (δ). The λ model alters each of the internal edges of the tree by multiplying them by λ by a value of 0-1. The branches to the tips of the tree remain as originally defined. The δ model allows for trait evolution to increase or decrease through time with values <1 demonstrating a decrease, >1 an increase. κ increases or decreases the branch lengths by the power of κ. This results in longer branches being increased/decreased to a greater degree than shorter branches.

The other models were as follows: the Ornstein-Uhlenbeck (OU) model which is represented by a random walk model but with phenotypes focusing towards an optimal condition (Butler

& King, 2004); the Early Burst (EB), also called the Accelerating Decelerating (ACDC), model is a model of exponential increase then slowing through time (Harmon *et al.*, 2010); finally, the "white noise" model is where there is no phylogenetic signal (all species are from the same normal distribution) (Harmon *et al.*, 2015).

2.7 Habitat filter

The United States Geological Survey (USGS) data (USGS, 1999) was used as the base for the habitat specificity for each species. 197 land cover types were recoded to four categories: closed (denoting forest); open (grassland, savannah, open woodland); human (built up areas, areas dominated by cropland); and land cover types not found in Africa (see Appendix 9-2 for mappings). Each species' existing range was assessed against the habitat types after removing human areas. Those species with over 90% of either open or closed habitat type were classed as habitat specialists in that category, all others being generalists. In addition, all species that were considered browsers or frugivores were considered closed habitat specialists, and obligate grazers were open habitat specialists (see Gagnon and Chew, 2000). When producing the forecast models specialist species (either closed or open specialists) had an additional barrier to dispersal, that of habitat (i.e. they cannot cross into unfavourable habitat).

Plants disperse as animals do, however, most are not expected to keep pace with climate change (Corlett & Westcott, 2013). There are currently few continent-wide projections for African vegetation, and where they do exist they are at a coarse scale and model a limited number of time periods, vegetation types, or ecosystems (see Sato & Ise, 2012; Gonzalez *et al.*, 2010; Alo & Wang, 2009). For these reasons, the habitat filter is static in that there are no projected vegetation changes in line with CO_2 or climatic changes which affect vegetation growth and structure (Malhi *et al.*, 2013). This makes the assumption that the lag in vegetation change will limit the spatial response of animals to climatic change.

2.8 Area connectivity and dispersal ability

Java programs (Oracle, 2012) were developed to model the connectivity and dispersal ability of each species. Connectivity was assessed to find areas of suitable climate that were connected to the original species distribution. It was also rechecked at each time period to assess which areas would be connected to the future climatically suitable areas. Those areas not connected were removed from statistical analysis except for chapter six (see Figure 2-5 for connectivity assessment). There are two uses for the connectivity assessment:

1. To find the envelope modelling approaches starting position. All climatically suitable areas, based on the GLM model, that are connected to the original IUCN distribution are designated the starting position for the envelope approach.
2. To find the areas that are climatically suitable in the future and that are connected to the previous time period's distribution. For example, to determine which 2030 areas are connected to the present day IUCN distribution or the area defined by the envelope modelling approach above (1).

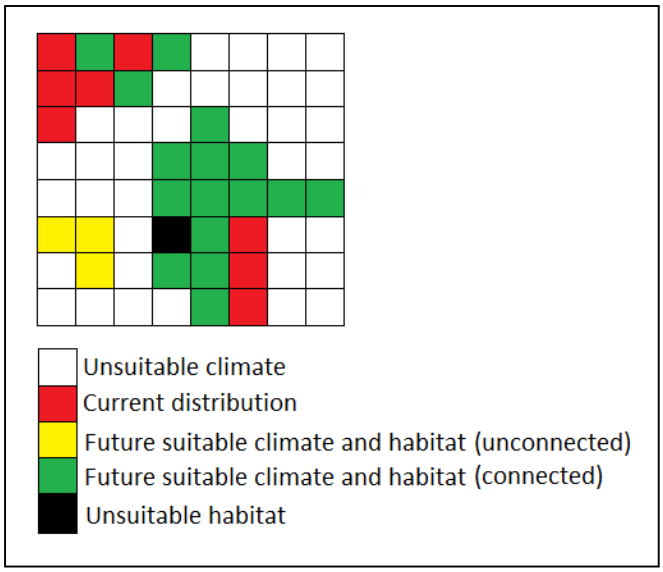

Figure 2-5: Connectivity assessment. Connected areas (green) are those areas directly connected to the current distribution (red) or via links by other connected cells. Other areas predicted as suitable but without connectivity are removed (yellow)

To establish connectivity the following process took place:

1. For each grid cell with current distribution (red in Figure 2-5) all surrounding eight cells in turn are checked to see if they are:
    a. Part of the current distribution (red)
    b. Part of the predicted suitable areas (yellow or green) and, if the habitat filter is present (see 2.7), have suitable habitat. The habitat filter assesses whether a cell has either (i) open or closed habitat unsuitable for species that are habitat specialists, and (ii) area that is deemed to be unsuitable due to human presence/land use
2. If the assessed cell is found to be predicted as suitable (i.e. not currently present), and with suitable habitat, then the cell is set as connected (green) and a repeat process starts from that cell to check the surrounding eight (hereafter called 'respawning'). Respawning continues until no other cells are found with suitable

climatic conditions ('exhaustion'). This takes place immediately before checking the remaining eight surrounding cells.

3. Upon exhaustion, the process returns to the cell that originally spawned the process and continues with its checking of its surrounding cells, some of which may already have been checked and are ignored.

Figure 2-6 demonstrates this process. Starting from the red cell 'S', cell 1 is checked. This is suitable and therefore respawning takes place and cell 1.1 is checked. This is not suitable so cell 1.2 is checked. This is suitable and respawning occurs again. Cells 1.2.1, 1.2.2, and 1.2.3 are unsuitable as is 1.2.4 due to incompatible habitat. Cell 1.2.5 is suitable and a further respawning would occur here (not shown).

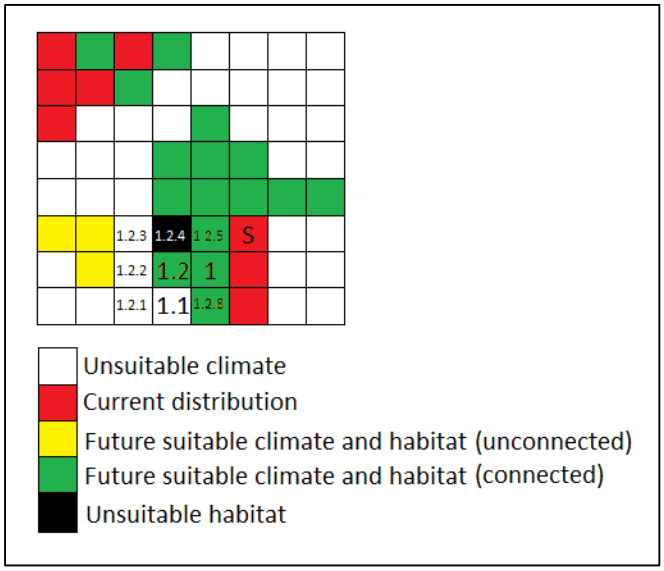

Figure 2-6: Calculating the connectivity for a species starting from cell (S) and the route that the cells are checked thereafter. The first cell checked is "1", then 1.1 which is not suitable, then 1.2, which is suitable and spawns further checks around itself (1.2.1, 1.2.2, etc.). Through this respawning process all adjacent cells to a suitable cell are checked.

Dispersal ability is modelled in the optimistic approach whereby each species has a yearly dispersal velocity based on mass (based on Schloss, *et al*., 2012; see Equation 2-1).

$$D_{HerbOmn} = 1.45 * M^{0.54}$$

Equation 2-1: Dispersal ability equation from Schloss, et al. (2012)

Where $D_{HerbOmn}$ is the yearly dispersal distance in kilometres, for an herbivore or omnivore, where M is body mass in kilograms (Schloss *et al.*, 2012). Given each species' yearly dispersal velocity it was able to travel a maximum distance multiplied by 30 for the first two time periods (2010-2039 and 2040-2069), and 20 for the final each given time period (2070-2089);

i.e. multiplied by the number of years within that climatic period. This limits the ultimate distance that a species can disperse and reduces the number of connected cells.

The methodology to predict the range a species will populate when limited by dispersal depends on establishing connectivity as above. Each time a cell is identified that has suitable climate, the distance to that cell is recorded. There are approximately 18km between adjacent grid cells, or 25km for diagonally adjacent cells (New, *et al*., 2002; see Figure 2-7). There may be more than one route to any cell; therefore the minimum value was recorded and retained for each cell. If when assessing the cell the current distance was greater than the minimum value, the process ended because a previous process would have already assessed all other dispersal routes.

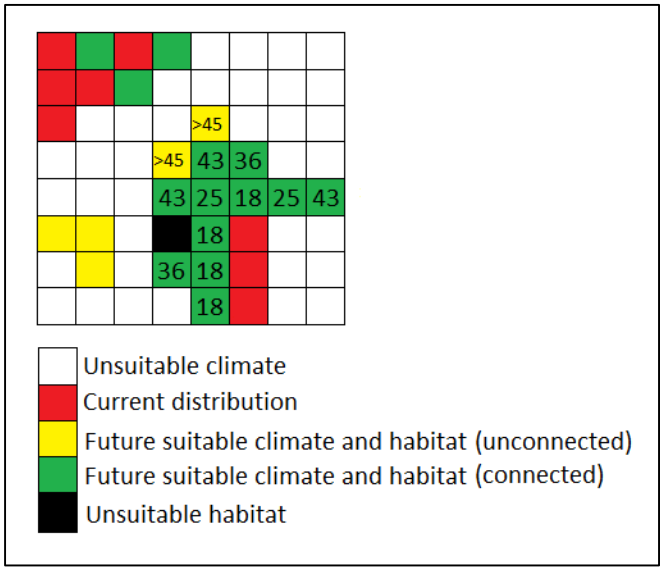

Figure 2-7: Calculating the dispersal of a species from the red cells. For a theoretical species with a maximum dispersal of 45km over 30 years the species could reach all green cells in that period. This highlights potential areas that are suitable but not reachable by the species. The numbers represent the distance travelled to a cell in km where 18km is the approximate distance between cells.

It is recognized that there may be many other components and attributes to the dispersal of a species including natal dispersal ages, gender differences, and social organization. While the causes of dispersal have been comprehensively explored, dispersal distance remains largely unstudied in antelope species. Most studies of mammalian herbivore dispersal have focused on rodents and lagomorphs (Schloss *et al.*, 2012; Sutherland *et al.*, 2000). For this reason the Schloss, Nuñez & Lawler equation is applied for all antelope species.

3. Antelope distributions: Establishing relationships between antelope distributions and species biological traits

Abstract

The distribution and diversity of species has been an area of biological study for centuries. Biogeographers seek to understand the drivers of geographical distributions based on geological and biological knowledge. Species distributions are largely determined by climate which has led to the development of species distribution models (SDMs). SDMs are empirical models that correlate environmental predictors with species observations in the field, and are used in many fields of research such as understanding species ecological dependencies and niches. This study develops SDMs for 73 of Africa's antelope species that inhabit most of the continents' diverse climates and habitats. I derive each species' optimal climatic conditions from the SDMs and, accounting for phylogeny, I explore the relationships between these climate and biological traits to identify variables that predict distribution patterns and species richness.

Hypotheses and predictions are made, based on our existing ecological and physiological knowledge of mammals, which link biogeographical and biological traits with the optimal climatic conditions for species. The results identify a non-linear relationship where precipitation predicts global range of species with a peak at approximately 800mm/year precipitation. A similar relationship is found with species diversity where a generalized additive model indicates peak diversity at approximately 1,000mm/year precipitation. The percentage of grass in a species' diet and adult body mass are correlated with a species' optimal temperature range. This relationship indicates larger species, with greater quantities of grass in their diets, are found in areas with larger temperature ranges, such as those found in savannah areas, compared with smaller temperature ranges found in forests. In general though, the lack of strong relationships between climatic conditions and biological traits suggests that antelopes have evolved a variety of adaptations that allows species of varying sizes and ecological requirements to exploit the wide range of climates that Africa provides.

Introduction

The diversity and distribution of species has captured the attention of researchers for centuries. That species have evolved, and thrive, within a distinct range of environmental conditions continues to stimulate avenues for research. Species distribution models (SDMs) are empirical models that correlate environmental predictors with species observations in the field (Guisan & Thuiller, 2005), and are now commonly used in this field of research. There are many uses for SDMs including the discovery of new populations or occurrences (Särkinen *et al.*, 2013; Williams *et al.*, 2009; Raxworthy *et al.*, 2003), understanding species ecological dependencies and niches (Elith & Leathwick, 2009), and projecting species future distributions based on climate projections (Milanovich *et al.*, 2010; Thuiller *et al.*, 2006a; Thomas *et al.*, 2004; Thuiller, 2004). This study develops models that predict the distribution of African bovids, a key group of species throughout the continent, including 73 species of antelopes and the African buffalo (see Appendix 9-1 for list of species). Using these models I explore the relationships between species climatic preferences and biological traits to identify variables that predict species presence and richness. I also investigate how confidence in the models may be affected by the characteristics of a species' range in relation to its size and fragmentation.

The study of species richness, clines of diversity, and the distribution of species based on environmental predictors has been ongoing for over a century (Grinnell, 1917; Wallace, 1860). Recently, much of this work has focused on the conservation of these species, understanding why areas are biologically diverse, and which areas require protection. Fundamentally, species distributions are bound by climatic conditions, although many other biotic and abiotic factors influence a species' range (Quintero & Wiens, 2013; Whittaker, 1975; Pienaar, 1974; Janzen, 1967; Grinnell, 1924; Von Humboldt & Bonpland, 1805). This link to climate has resulted in the development of modelling methodology that produces correlative models which describe species distributions; these are commonly referred to as species distribution models. The history and evolution of SDMs has included three main phases: (a) the development of non-spatial, species-environment relationships based on empirical data, (b) spatial modelling of species distributions based on expert opinion, and (c) spatially explicit, empirical models of species distributions (Guisan & Thuiller, 2005). Species distribution modelling, as spatially explicit, empirical models, have assumed many guises, approaches, and names over the years, and it is important to understand which method is in use and how each method might alter the perception of the results. Araújo and Peterson

(2012) provide a valuable review of the different modelling approaches that are often found under the banner of SDMs. These include "Species-distribution models", "Habitat-suitability models", "Ecological niche models" (also climatic niche and niche models), and "Bioclimatic envelope models" (also species-climate envelope models, climate envelope models). As this area of research continues to mature, different approaches to a common problem have led to increasingly complex methods. Originally based on climate variables alone, climatic envelope models (CEMs) produced models describing the *Grinellian niche* (or *fundamental* niche) where a species occurs wherever suitable environmental conditions are present (Guisan & Thuiller, 2005). Developments and accessibility to new sources of data have resulted in the addition of habitat suitability data, species trait and behavioural data, and details of species interactions, such as predator/prey relationships and various forms of symbiosis. These models produce results closer to the *realized niche* described by Hutchinson (Guisan & Thuiller, 2005). These have been labelled by some as habitat suitability models (see Araújo & Peterson, 2012), but have also been included as an extension of SDMs (Guisan & Thuiller, 2005). There are many examples of the inclusion of different types of data and processes beyond climatic: remote sensing imagery (often vegetation indices) (Cornuault *et al.*, 2013; Kurtz *et al.*, 2010), soil and nutrients (Thuiller, 2013; Stanton *et al.*, 2012; Coudun *et al.*, 2006; Iverson & Prasad, 1998), predator-prey interactions (Trainor *et al.*, 2014), topographical features (Guisan *et al.*, 2007; Iverson & Prasad, 1998), disturbance (Thuiller *et al.*, 2006a), light (Guisan *et al.*, 2007; Coudun *et al.*, 2006), and vegetation type/land use (Stanton *et al.*, 2012; Iverson & Prasad, 1998). While there may be advantages to including these predictors in some models, they are not all universally suitable for all species and variables must be considered for their relevance to the species being studied (Guisan & Thuiller, 2005). Also, where SDMs are being used to predict the future distributions of species, dynamic variables (such as vegetation indices, disturbance, land use, and predator-prey interactions) also require projections to match climate predictions potentially leading to greater uncertainty. Static variables can improve model performance (Stanton *et al.*, 2012), but in all cases a thorough analysis of predictive variables is required based on the species being modelled. The SDM examples above relate to species from the Animalia and Plantae kingdoms, but they have also been used in modelling fungi such as the death cap mushroom (*Amanita phalloides*) (Wolfe *et al.*, 2009) highlighting the comprehensive application of such models.

The development of species distribution modelling has not simply been a case of adding more data or variables; the underlying methodology has also been altered. This is

particularly evident when considering ecological niche models (ENM). With ENM the modelling of complex processes that define species distributions requires interpretation and hypothesis relating to the focal species (Peterson & Soberón, 2012). This is far removed from the bioclimatic envelope approach that models a distribution based on observations of species distributions and climate. All methods seek to achieve a similar goal, that being to develop robust models that predict species distributions. To achieve this goal, it is important to understand which modelling technique will best suit the research at hand and which variables best predict the distribution of the taxa studied (Guisan & Thuiller, 2005). Here I evaluate both biotic and abiotic variables before identifying climatic variables that are best suited to model a wide range of antelope species.

There is ongoing debate on the transferability of models (Randin *et al.*, 2006), to what extent results are affected by variable selection (Ashcroft *et al.*, 2011) and the scale used (Randin *et al.*, 2009). In spite of this, many agree that climatic conditions, to a large extent, delimit species distributions and range, and density (Owen-Smith, 2002) of species. Climate may directly influence distributions via physiological limitations, or indirectly via resource distribution. Climate may also influence sympatric species triggering indirect consequences on the focal species that may be positive (mutualistic species) or negative (competitors, predators) (Thomas, 2010). Evidence of species range shifts and localized extinctions, driven by climate change, are no longer theoretical and have been reported for many taxa highlighting the importance of climate in the distribution of species (Lehikoinen *et al.*, 2013; Moritz *et al.*, 2008; Franco *et al.*, 2006; Parmesan, 2006; Parmesan & Yohe, 2003).

Here, I develop models that predict the distributions of Africa's antelope species and the African buffalo. This important group of species act as environmental architects, seed dispersers, prey, and as a food source for indigenous human populations. They are an often overlooked group that offer great biological diversity in morphology, ecology, and behaviour, thus providing an excellent candidate group to identify relationships between species traits and variables that define their distributions. A wide array of threats faces Africa's antelopes and has led to 63% of species populations being in decline, and 23% of species being threatened (IUCN, 2014a).

Establishing which variables, whether biotic or abiotic, best predict antelope distributions is fundamental when identifying current and future species distributions. Previous studies of African antelopes have demonstrated both climate and soil as important predictive variables (Hopcraft *et al.*, 2009; East, 1984), with Singh & Milner-Gullard (2011) providing evidence

that human disturbance has an impact on distribution. Pettorelli *et al.* (2009) showed how satellite derived vegetation indices can be useful in establishing the ecological basis for antelope distribution. Here we evaluate 40+ variables including climatic, abiotic, and vegetation indices, before selecting a common set that best predicts the current distribution of species. Evaluated variables include continuous (climate, vegetation indices, soil nutrient fixing potential) and factorial variables (soil type, habitat type). I assess the importance of the variables in predicting antelope distributions using principal components analysis (PCA), and evaluate the strength of the models using area under the curve (AUC) (Thuiller *et al*., 2006), specificity, and sensitivity measures (Swets, 1988). Through this process I produce models that are both accurate and that have sound biological meaning.

One of the aims of this study was to identify the optimal climatic values for each species based on the models. Antelope species have evolved adaptations that enable them to be present across Africa's wide diversity of ecosystems and climates from the very hot and arid deserts, to high rainfall tropical rainforests, to the high elevations found in Ethiopia's mountains. This spatial diversity, coupled with their ecological, morphological, and behavioural diversity, offers the opportunity to identify relationships between species trait data and climatic conditions that may be applicable, and bring understanding, to other taxa globally. Therefore, the optimal conditions of species were analysed in conjunction with species trait data to establish correlations. Because species groups may share traits as a consequence of relatedness rather than as a reflection of evolutionarily independent events, I performed these analyses controlling for the effect of shared ancestry (Pagel, 1992; Felsenstein, 1985). I also investigate precipitation as a driver for species richness and review how differing diet specialists are associated to different levels of precipitation. Such links could prove important in light of future climatic change in assessing which species could prosper and which may be at increased risk.

Linking climatic conditions with species trait data

Areas of low and high rainfall present habitats that may favour specialist feeders, particularly browsers (arid) and frugivores (wet). In very arid conditions little grass is available, shrubs tend to dominate, and vegetation is widely distributed (Burgess, 1995; Whittaker, 1975). Similarly, while the peak of plant species diversity is found in high rainfall, low latitude areas in Africa (Linder, 2001), these areas have restricted foraging options for antelopes as little grass is present (Bodmer, 1990; Whittaker, 1975). Savannah and woodland areas in mid-rainfall areas (approximately 1000mm annual precipitation) present all foraging options for

antelopes; those being fruit, grass, and browse (East, 1984). Therefore it is posited that specialist feeders will be found at either end of the precipitation scale and a more generalist diet would be found in areas with more varied dietary options (H_1). It is predicted that species diet diversity, measured using the Shannon Weaver diversity index, will peak in areas where species can consume a wider array of vegetation (P_1). This is due to the need to specialize, and thereby have low diet diversity, in areas of low and high rainfall where species might specialize towards browsing and frugivory respectively. This does not preclude specialist feeders in savannah and woodland areas, but allows for more generalists utilising all food resources in addition to the specialists.

There are many theories that attempt to explain species diversity. One theory suggests high diversity is linked to stable climatic conditions and high tropical plant productivity. These conditions result in opportunities for species to co-exist, and specialists to evolve (Cox & Moore, 2005; Osbourne, 2000). Various studies have found flora diversity to be higher in rainforest areas (Linder, 2001; Chapman *et al.*, 1999) increasing with levels of rain up to 2000mm/year (Kay *et al.*, 1997). In primates this 2000mm/year is the limiting factor above which species richness declines (Kay *et al.*, 1997). However, as stated above, grass is not typically found in forests and this potentially restricts the diversity of species that forage upon it. Bodmer (1990) demonstrates this where grazing and browser/grazer ungulate species are seldom found in dense tropical forests due to a lack of forage which reduces species diversity. Furthermore, East (1984) found in his study on African savannah herbivores including many antelopes, that a wider variety of feeding habits was found in arid savannah species (peak biomass of those species found where annual rainfall <820mm) compared to moist savannah species (peak biomass ≥1000mm). Greater foraging selectivity in grazing species was found in the moist savannah species. Greater selectivity suggests increased specialization and potentially more grazing species in these wetter areas before trees begin to dominate and grass is lost. Whittaker (1975) demonstrates that the change in vegetation to forest occurs when annual rainfall reaches approximately 1,350mm. Therefore, it is hypothesized that antelope species diversity will increase with annual precipitation before peaking in areas where the widest selection of dietary options is present (H_2). Where East's (1984) study focused on the savannah species, this hypothesis extends to desert and tropical rainforest areas as greater specialization is required in those areas. It is predicted that the peak of diversity should occur at a point where the dry savannah, i.e. where the widest range of feeding habits is found, crosses over to a larger grouping of specialist grazers in the wet areas (P_2). Species diversity should then fall as precipitation

increases and forests begin to dominate. H_2 contradicts the stable climate and plant productivity theory, as well as the results from plants; however, it fits with our ecological knowledge of antelopes, and the diversity of resources available to this terrestrial group of species.

Tropical forest areas provide a stable climate identified by low ranges in temperature and relatively high levels of rainfall (Cadena *et al.*, 2012; Janzen, 1967) that influence the diets of inhabiting species. Further to H_1 and H_2 above, areas with high rainfall and a dominance of tree flora provide more fruit than in open habitat, and less grazing opportunities (Bodmer, 1990). Therefore species in high rainfall areas should have high percentages of fruit in their diet (P_3). This can be extended to hypothesize a negative relationship between optimal range of temperature, and high percentages of fruit in the diet as tropical forests are characterized by relatively stable temperature (H_3).

Some antelope species have adapted to the dense forests, determined by high rainfall areas. The manoeuvrability hypothesis describes how smaller body size aids those species in dense habitat via improved concealment and movement (Bro-Jørgensen, 2008). Therefore negative relationships between precipitation (predicting variable) and body mass and shoulder/horn length ratio, is expected (P_4). This would also agree with previous comparisons between forest and plains antelope species (Estes, 1991) and body mass/diet comparisons of antelopes and ungulates (respectively Gagnon & Chew, 2000; Bodmer, 1990). Species with greater mass, and therefore body size, also have reduced body surface to volume ratio compared to smaller species. This results in smaller species losing proportionally more water through evaporation. Larger species, however, profit from being able to absorb heat during the day which benefits them through colder nights (Schmidt-Nielsen, 1990). It is hypothesized (H_4) that smaller antelope species should be found in areas that provide shade, thus avoiding absorption of solar energy, and stable areas with less variable temperature; both are forest attributes. Larger species would therefore be better suited to open areas that experience greater fluctuations in temperature both daily and annually. This corresponds with areas to the north and south of the equatorial tropical rainforests, and generally agrees with the principles of Bergmann's rule (see translation in James, 1970; Ashton, *et al*., 2000). This hypothesis is compatible with the manoeuvrability hypothesis and they are not considered mutually exclusive. It is therefore predicted that body mass will be positively correlated with the temperature range experienced by species

(P_5). The temperature range for each species being derived from the difference between optimal coldest and hottest conditions based on the models.

In summary, this chapter develops species distribution models to determine factors affecting the distribution of African bovids and test related hypotheses. By identifying species optimal climatic conditions, and correlations between those conditions and species traits, I hope to develop our understanding of this important group of animals. This knowledge, and the models developed, contribute to the other chapters of this thesis as I identify species that are threatened due to the potential impact of climate change.

Methodology

Study species

The distribution of 74 members of the bovidae family, i.e. 73 antelope species and the African buffalo, were extracted from International Union for the Conservation of Nature (IUCN) distribution maps (IUCN, 2011). This group represents all of Africa's antelope species where distribution maps were available and the African buffalo, but excludes members of the Caprinae subfamily which includes goat, sheep, and ibex species. This IUCN dataset provides distributions for species where their presence is considered (a) extant, (b) possibly extant, (c) possibly extinct, (d) extinct, and (e) uncertain. Here, species are considered present based on their extant distribution and, assuming the species was absent from all other areas, a presence/absence binomial distribution was derived for each species. Species were only considered present if they were native to those areas, thereby excluding populations reintroduced into non-indigenous areas. IUCN distribution maps are provided as ESRI native format shape files depicted as polygons. The polygons were rasterized to a 10' grid scale (i.e. ~344km^2 at the equator) to match the climate dataset (see 2.5.1) providing presence/absence in each grid cell. The IUCN threat status for each species was also obtained and correlated to species distribution size, based on the number of present 10' grid cells (hereafter cells), using Pearson's product-moment correlation.

Species distribution models

The R package BIOMOD (Thuiller *et al.*, 2009) was used to create the species distribution models based on three predictive variables: Natural log of annual precipitation, hottest monthly temperature, and coldest monthly temperature. These variables were selected from over 40 assessed based on PCA, variable importance assessment within the models, the availability of continent wide data for the present and future (for use in further studies), and

biological importance (see 2.5.3 for further details). Quadratic generalized linear models (GLM) were selected to produce the models representing the species distributions (see 2.2 for modelling selection). The GLM models were calibrated using a random sample of data (70%) and stepwise GLM method (stepAIC search method "both") resulting in the most parsimonious model based on AIC (Thuiller *et al.*, 2003). The models were then evaluated against the remaining 30% of the data using AUC, sensitivity, and specificity (Swets, 1988).

To account for the environmental human footprint and its impact on species presence, a land transformation (LT) weighted filter was applied (see 2.5.2) following Thuiller *et al.* (2006). The human footprint dataset (Sanderson *et al.*, 2002) is based on four types of data used as proxies for the impact humans have around the world. These four data types are: land transformation, population density, accessibility, and electrical power infrastructure. The human footprint data provides a sense of the ecological footprint of humans (Thuiller *et al.*, 2006), and the application of the filter seeks to represent human influence, and restrictions placed on the presence of wildlife.

Data acquisition and identification of species-specific optimal climatic conditions

Optimal values for each climatic variable are generated for each species. Using the model intercept and coefficients the vertex values provide the optimum value (see 2.2) which is then evaluated against species trait data. For some species the optimal value for a variable could not be set because (a) the variable was not present in the model due to being dropped in the stepAIC process, or (b) the calculated value was outside the range of values found in Africa.

The species trait data includes ecological (diet diversity, percentage of grass, browse, and fruit in the diet (Gagnon & Chew, 2000)), morphological (adult mass, horn length/shoulder height index), and behavioural (group size) characteristics of the species (Bro-Jørgensen, 2008; Bro-Jørgensen, 2007; Bro-Jørgensen, unpublished; Kingdon, 1997), as well as global range size defined as the number of cells derived from the rasterization of the IUCN distributions. Diet diversity is calculated using the Shannon Weaver diversity index (see Equation 3-1) where H' is the Shannon Weaver diversity index, and p_i is the relative proportion of each diet type (grass, browse, and fruit).

$$H' = -\sum p_i \ln(p_i)$$

Equation 3-1: Shannon Weaver diversity index where H' is the Shannon Weaver diversity index, and p_i is the relative proportion of each diet type (grass, browse and fruit).

Generalized additive models (GAM) were used to investigate the relationship between annual precipitation and species diversity (splines = 4) (Hastie, 2011). Based on the existing species distributions, for each cell, the number of species was correlated with the annual precipitation. A smoothed curve was produced using the model and divided into 500mm/year segments. Within each of these segments the proportion of antelopes from each dietary group (see Gagnon & Chew, 2000) was calculated to identify the dietary diversity within each segment.

Comparative analysis

Antelopes are grouped in distinct tribes with similar morphological features. All behavioural, ecological, and morphological analyses were conducted with and without control for phylogeny to examine the effect of correcting for non-independence of data (Martins & Hansen, 1997). Different evolutionary models were used for different variables with bivariate and multivariate analyses using the R packages gls and pgls (see 2.6; Table 2-3).

Bivariate regression and multivariate regression were used to correlate climate variables with species trait data in R with and without phylogenetic control. Multivariate analysis assessed climatic variables as dependant variables whereby species traits predicted climatic values. Stepwise regression was used to find the best model for each variable based on the species dietary variables (percentage of fruit, browse, grass in the diet, and diet diversity), group size, horn length/shoulder height index , and the log of mass (quadratic and linear). Models predicting the log of global range and diet diversity were also produced based on climatic, dietary (for the global range model only), and body mass variables before stepwise regression.

Stepwise regression, based on AIC, computes the best fitting model ("stepAIC" function, direction=both: "MASS" R package (Venables, 2002)). There is no equivalent stepwise regression method for pgls; for this reason forward and backward stepwise regression methods were developed to find the best phylogenetic models based on improving AIC results.

Multicollinearity was identified performing variance inflation factor ("vif" function in the "car" R package (Fox & Weisberg, 2011)) tests on the data set where a value of >10 demonstrates multicollinearity (but see O'Brien, 2007). A specific concern was the diet variables and diet diversity being correlated. High levels of collinearity can result in high variance inflation factors which can lead to artificially high R^2 values where no model variable

is significant. This can produce models where a small change in data has large changes in predictive estimates (O'Brien, 2007). This is taken into account when assessing the models.

Correlation strength was measured using R = $\sqrt{adjusted\ R^2}$ to define the strength of a correlation following Fowler, *et al*. (1998).

Definitions

Table 3-1 gives the six different foraging strategies displayed by antelopes as referred to in the study of all extant members of the bovidae family by Gagnon and Chew (2000).

Diet Type	Definition
Obligate grazer	>90% monocots
Variable grazer	60-90% monocots
Browser-grazer (intermediates)	30-70% monocots and dicots, <20% fruit
Generalist	>20% monocots, dicots and fruits
Browser	>70 dicots
Frugivore	>70% fruit, little or no monocots

Table 3-1: Definitions of antelope diet type from Gagnon and Chew (2000).

"Range fragmentation" refers to the number of separate areas in Africa where a species is present or predicted to be.

Results

Model performance and refinement

A model with an AUC score of 0.5 indicates that the model is no better than a random model; a score of 1 indicates perfect prediction by the model (Swets, 1988). The AUC scores were categorized according to their accuracy following Swets (1988). The categories are "Low [accuracy]" (0.5 < AUC ≤0.7), "Useful [for some purposes]" (0.7 < AUC ≤0.9), and "High [accuracy]" (AUC > 0.9). The mean AUC score for the models was 0.958 (s.d.=0.033, min=0.50 [*Oryx dammah*], max=0.999 [*Beatragus hunteri*]). Figure 3-1 (left) shows that only *O. dammah* fell into the "Low" category and three species fall in the "Useful" categorization as described by Swets (1988). For this reason *O. dammah* is removed from any further analysis. The "Useful" modelled species are the hartebeest (*Alcelaphus buselaphus*), topi (*Damaliscus lunatus*), and the African buffalo.

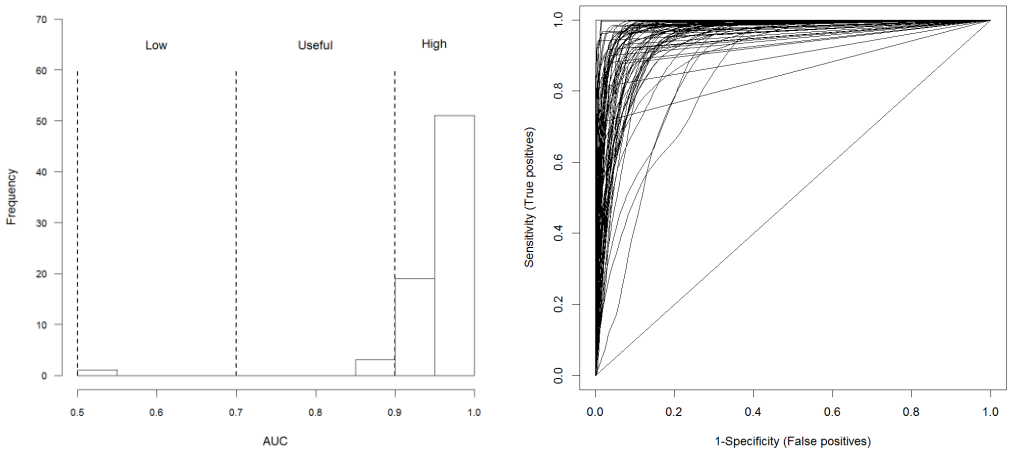

Figure 3-1: Model performance. Left: Histogram displaying the model Area Under the Curve (AUC) values for the Receiver Operating Characteristic (ROC) for each of the species models. Vertical bars denote the number of models found within usefulness categories as described by Swets (1988). Right: ROC curves for all species. Lines closer to a 45° line indicate poorer fitting models. Note Oryx dammah represented by the 45° angle line.

There is a significant negative linear relationship between range fragmentation and the model performance (AUC) ($p<0.003$; $R^2=0.444$; see Figure 3-2: left), signifying that as fragmentation in range increases the performance of the model falls. There is also a tendency towards lower model performance for species with larger ranges [model = $\sim \log(range\ size)^2 + \log(range\ size)$] ($p<0.001$; $R^2=0.198$; see Figure 3-2: right). In addition, there is an unsurprising significant negative correlation between species range size in grid cells and IUCN threat status ($r= -0.726$; $p<0.001$).

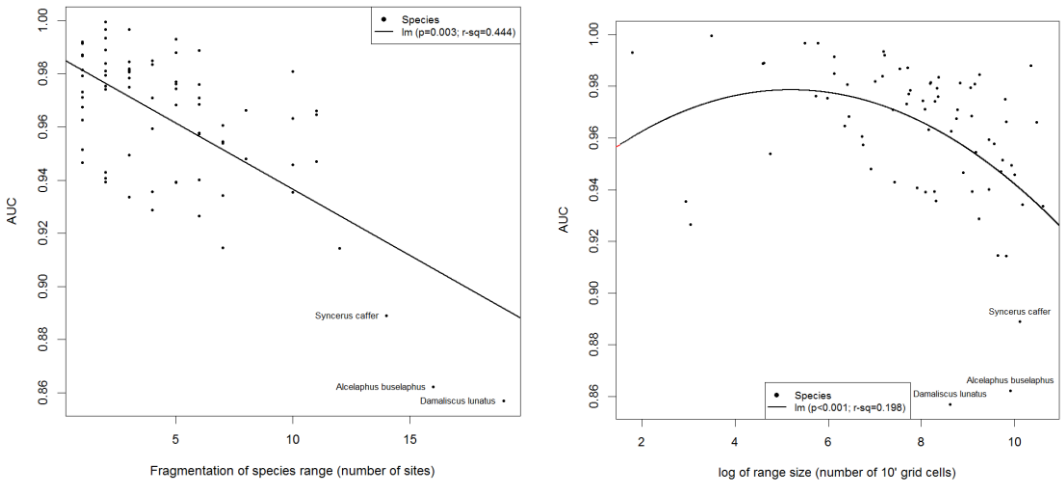

Figure 3-2: Left: Linear model of fragmentation of species ranges against AUC. Range fragmentation is defined as the number of sites identified from the IUCN distribution. Right: Natural log of range size against the AUC score for the models. The line represents a quadratic relationship (AUC=log(range size)²+log(range size)).

Species richness and rainfall

The BIOMOD variable importance command demonstrated that annual precipitation was the most important variable for the distribution of 49 of the 74 species. Principal components analysis confirmed the importance of annual precipitation as part of principal component 1 (see 2.5.4). Analysis of the individual 10' grid cells (~344km^2 at the equator) gives a maximum number of species in a cell as 23 (mean=6.062; s.d.=4.914) with the greatest diversity being centred on Kenya and Tanzania (Figure 3-3 Left). Analysis by GAM of increasing annual precipitation in 500mm/year increments, species richness, and diet type demonstrated that highest species diversity is found at approximately 1,000mm/year annual precipitation (Figure 3-4). Diet diversity varies greatly within the 500mm/year increments with browsers and variable grazers being the only common diet types across the annual precipitation range (Figure 3-4 & Table 3-2). Frugivory becomes the dominant feeding style above 1,500mm/year annual precipitation, while generalists and browser/grazers are only present up to 1,500mm/year annual precipitation. There is a trend towards less variance in the diet percentages in the mid precipitation sub-divisions (>500 &≤1,000mm/year and >1,000 &≤1,500mm/year) compared to the high rainfall areas (>3,000mm/year) (respectively (F-tests): F (1, 5) = 7.486, p= 0.063; F (1, 5) = 7.848, p= 0.057). This difference is not seen in comparisons between low (<500mm/year) and mid precipitation areas (p=0.48 [>500 & ≤1,000]; p=0.511 [>1,000 &≤1,500]).

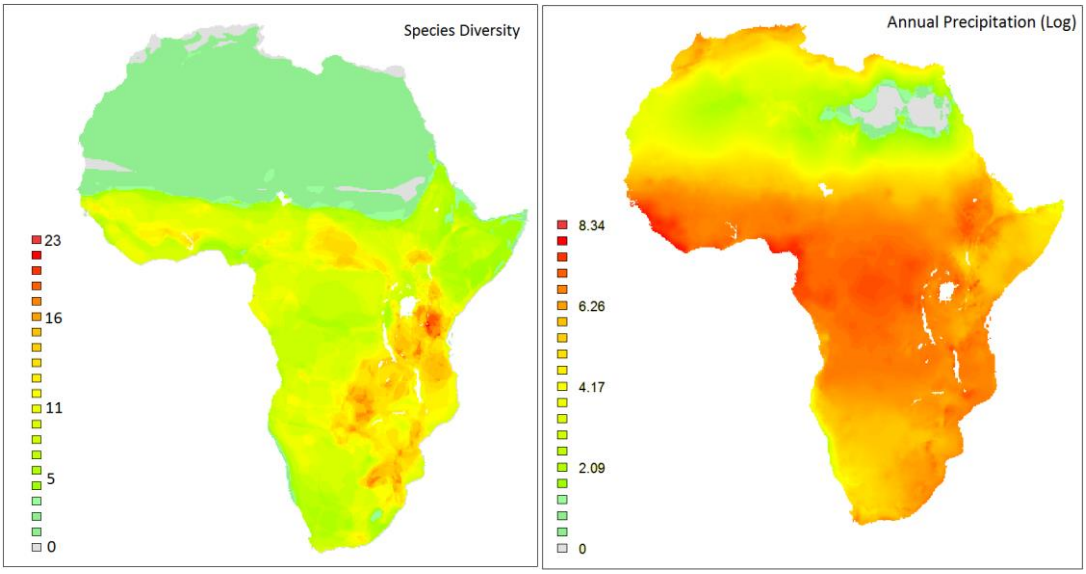

Figure 3-3: Left - Current antelope species diversity derived from IUCN data. Right – Natural log of current annual precipitation (mm/year for 1950-2000)

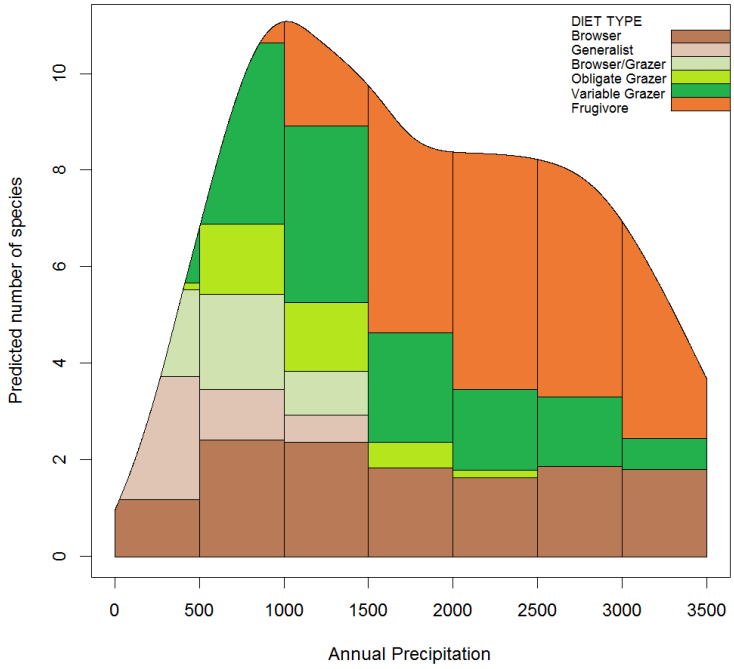

Figure 3-4: GAM prediction of the number of species related to the annual precipitation (mm/year) split into 500mm precipitation bands. Within the band is the distribution (proportion) of diet types (see Table 3-1 & Table 3-2).

Annual Precipitation	Browser	Generalist	Browser/ Grazer	Obligate Grazer	Variable Grazer	Frugivore
≤500	17.16%	37.49%	26.70%	2.00%	16.45%	0.20%
>500 &≤1,000	21.69%	9.47%	17.79%	13.20%	33.88%	3.97%
>1,000 &≤1,500	21.31%	5.07%	8.12%	12.87%	33.13%	19.49%
>1,500 &≤2,000	18.72%	0.94%	0.95%	5.49%	23.30%	50.60%
>2,000 &≤2,500	19.37%	0.39%	0.25%	1.79%	20.11%	58.07%
>2,500 &≤3,000	22.57%	0.00%	0.00%	0.32%	17.46%	59.65%
>3,000	25.73%	0.00%	0.00%	0.00%	9.27%	65.01%

Table 3-2: Percentage of species with certain diet types by annual precipitation bands.

Table 3-3 shows the uneven distribution of precipitation across Africa with large numbers of low rainfall grid cells compared to other areas.

Precipitation band (mm/year)	10' grid cells
0 to 100	26,405
>100 to 200	6,115
>200 to 300	4,737
>300 to 400	4,846
>400 to 500	4,308
0 to 500	46,411
>500 to 1,000	17,488
>1,000 to 1,500	15,040
>1,500 to 2,000	8,554
>2,000 to 2,500	1,226
>2,500 to 3,000	436
>3,000	225
Total	89,380

Table 3-3: The number of 10' grid cells in Africa split into annual precipitation bands (mm/year). Uneven bands are present to highlight the area of arid conditions in Africa.

Predictors of optimal climatic conditions for African antelope species

Table 3-4 and Table 3-5 present the linear and non-linear quadratic relationships between single species traits and the optimal climatic conditions for the species. Table 3-4 shows the results without phylogenetic control, whereas Table 3-5 includes phylogenetic control using the evolutionary models defined in Table 2-3 (see 2.6). Table 3-6 provides the sample sizes for each relationship. These differ due to missing data for species traits and the optimal value calculations as described in the methods. Table 3-7 presents the multivariate models predicting climatic conditions, global range, and diet diversity.

Comparative analysis without phylogenetic control

Bivariate relationships

Without phylogenetic control (Table 3-4) all variables provide a range of significant ($p < 0.05$) and very significant relationships ($p < 0.01$). The R^2 values for these models were generally low being <0.25 (see Appendix 3.1 for model R^2 values).

The quadratic relationship between temperature range and percentage of grass in the diet (R^2=0.441) produces a u-shaped (convex) parabola, with a nadir at approximately 5°C temperature range. There are no antelope species with a range below 4.6°C, therefore this demonstrates a positive relationship between temperature range and percentage of grass in the diet. This is to be expected as grassland/savannah areas have a greater range in

temperature than forests. Temperature range also produces positive linear relationships with adult mass (R^2=0.255), and group size (R^2=0.258). There were also highly significant positive relationships that had lower R^2 values between temperature range and horn/shoulder index (R^2=0.200), and a negative relationship between temperature range and percentage of fruit (R^2=0.225).

A quadratic relationship between annual precipitation and fruit percentage in the diet was found (R^2=0.172). When plotted this provides a convex relationship that suggests high fruit percentage in the diet at very low precipitation (i.e. log values 0-3.5 annual precipitation; see Figure 3-5). However, no species have optimal precipitation in this range and therefore the relationship represents a largely positive correlation between annual precipitation and percentage of fruit in the diet; hence a linear regression also provided a highly significant result (p=0.004; R^2=0.144). Figure 3-5 also shows two distinct groups of species that account for the high variance in the model. The first group, consisting largely of the duikers, have high fruit percentage in their diet and a higher optimal precipitation, the remaining species display greater variability on both axes.

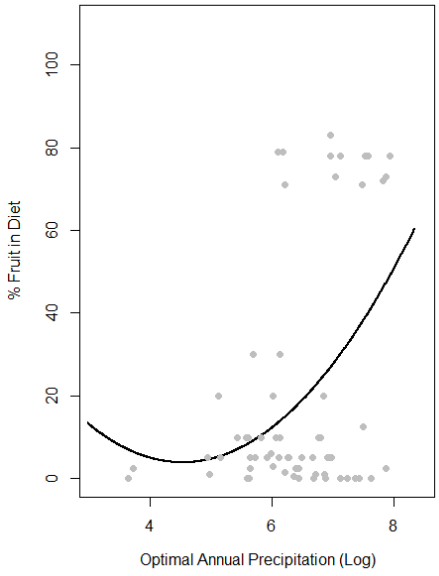

Figure 3-5: Percentage of fruit in diet predicted by optimal annual precipitation (p=0.003; R^2=0.172) of antelope species (grey filled circles).

There is an n-shaped (concave) shaped quadratic relationship between annual precipitation and percentage of browse but the correlation is modest (R^2=0.186). This relationship suggests that species preferring low to medium levels of precipitation have higher browse in their diet. As with the percentage of fruit relationship with annual precipitation, there is high

variance in the data. The positive relationship between annual precipitation and global range is weak (R^2=0.079).

There is variation in species with different mass and horn/shoulder index along the precipitation gradient and no linear relationship was found between these variables. This variation is demonstrated by the dik-diks (*Madoqua* genus), similar in mass to the forest duikers (Cephalophinae subfamily), that have evolved to live in more arid climates (dik-dik precipitation preference: n=4; mean=228.4±61.6(mm/year); range 143.0-290.1). In species preferring high rainfall (>2,000mm/year and suggestive of forest) there is a trend for species with a smaller mass compared to those under 2,000mm/year ($F_{(1,47)}$=3.575, p=0.065) and significant difference in horn ratio ($F_{(1,47)}$=11.304, p=0.002), but outliers exist such as the sitatunga (*Tragelaphus spekii*).

There were highly significant correlations between optimal coldest temperature and (a) grass percentage in diet (R^2 = 0.236) exhibiting a negative relationship; and (b) fruit percentage in diet (R^2 = 0.248) exhibiting a positive relationship. There were also significant negative relationships between coldest temperature and group size, and global range (R^2 = 0.089 and R^2 = 0.075 respectively). The relationships between coldest temperature and (a) adult mass, and (b) horn/shoulder index, are convex quadratic relationships. These relationships demonstrate species with larger mass and horn/shoulder index are found in areas with cooler temperatures. However, both relationships were weak correlations (R^2 = 0.157 and R^2 = 0.128 respectively).

Hottest optimal temperature showed two significant positive relationships, i.e. with the percentage of grass in the diet and the horn/shoulder index; however, only a modest proportion of variance in both variables was explained in this way (R^2 = 0.074 and R^2 = 0.075 respectively).

Multivariate analysis

The multivariate analysis (Table 3-7) produced significant results (p<0.05) for all models. The variance explained by the models differed, producing adjusted-R^2 values between 0.074 and 0.439. Note that below R^2 signifies "adjusted-R^2" for brevity.

The model of temperature range was highly significant (p<0.001; R^2=0.439). The model included the percentage of grass (linear and quadratic components) and adult mass (linear) as independent variables, where a greater percentage of grass (up to 74%) and adult mass predicts a larger temperature range.

The annual precipitation model produced similar results ($p<0.001$; $R^2=0.437$) including quadratic and linear functions of adult mass and percentage of grass, and the linear function of percentage of browse. The model predicts high rainfall areas correspond with least grass in the diet and high rainfall is linked to species with reduced body mass. Finally, the model predicts a high proportion of browse in the diet where there is lowest rainfall. Adult mass (linear) was not significant (0.101) but was retained by the model through stepwise regression.

Global range was best predicted by annual precipitation with both quadratic and linear being highly significant (model $p<0.001$). This model has a modest correlation ($R^2=0.294$) and predicts the largest range for species with an optimal precipitation of approximately 800mm/year. Diet diversity was predicted by hottest and coldest temperature, with temperature range and annual precipitation. This produced a modest correlation ($R^2=0.246$). Finally, both optimal hottest and coldest temperature were predicted by grass percentage in the diet, however, both correlations were weak to modest ($R^2 = 0.074$ and $R^2 = 0.201$ respectively).

Comparative analysis with phylogenetic control

Bivariate analysis

When phylogeny is controlled for (Table 3-5) the number of significant relationships and the R^2 values are greatly reduced (Appendix 3-1). The predictors of global range match those for the non-controlled data due to the lack of evolutionary signal. Moreover, there is a significant concave relationship, represented as a negative relationship within the values range, between annual precipitation and the percentage of browse in the diet ($p=0.011$, $R^2=0.117$). Percentage of grass in the diet shows a very weak negative relationship with coldest temperature ($p=0.032$, $R^2=0.010$) as well as a very weak positive relationship with temperature range ($p=0.032$, $R^2=0.011$).

Best model (not phylogeny controlled)

	APp	AP ^2 coef	AP coef	AP sig	HTp	HT ^2 coef	HT coef	HT sig	CTp	CT ^2 coef	CT coef	CT sig	TRp	TR ^2 coef	TR coef	TR sig
Adult Mass	0.776		2.41E-01		0.088		5.59E-02	.	0.011	-5.61E-03	5.50E-02	*	0.000		8.80E-02	***
Group Size	0.060	-3.27E+00	9.76E+00	.	0.071		4.98E-02	.	0.030		-5.12E-02	*	0.001		7.84E-02	***
Global Range	0.021		2.45E+00	*	0.281	6.88E-03	-4.93E-01		0.039		-8.19E-02	*	0.259		4.32E-02	
% Grass	0.515		-1.54E+01		0.037		1.74E+00	*	0.000		-2.40E+00	***	0.000	1.14E-00	-1.08E+00	***
% Browse	0.002	-1.01E+02	2.87E+02	**	0.057		-1.31E+00	.	0.598		3.00E-01		0.074		-1.08E+00	.
% Fruit	0.003	3.88E+00	-3.52E+01	**	0.481	-9.50E-02	5.88E+00		0.000		2.10E+00	***	0.001		-1.88E+00	**
Horn/Shoulder Index	0.136		-2.13E-01		0.034		1.12E-02	*	0.031	-1.46E-03	2.27E-02	*	0.002		1.35E-02	**
Diet Diversity	0.111		-2.23E-01		0.193		-6.57E-03		0.141	-1.12E-03	2.13E-02		0.333	-7.86E-04	2.57E-02	

*Table 3-4: The best linear or quadratic model for the relationship between species trait and optimum climatic variable for species. AP – Annual Precipitation, HT – Hottest Temperature, CT – Coldest Temperature, TR - Temperature Range, AP**p=** Annual Precipitation p-score for the model, AP**coef** and AP^2**coef** - the Annual Precipitation coefficient for the model denoting positive/negative relationship (note where there the AP ^{2} coefficient is present, the best model is quadratic, otherwise linear), AP**sig** – Annual Precipitation significance where . (point) <0.1, * <0.05, ** <0.01, *** <0.001. Sample sizes (n) values for each relationship are found in Table 3-6.*

Best model (phylogeny controlled)

	APp	AP ^2 coef	AP coef	AP ML	AP sig	HTp	HT ^2 coef	HT coef	HT ML	HT sig	CTp	CT ^2 coef	CT coef	CT ML	CT sig	TRp	TR ^2 coef	TR coef	TR ML	TR sig
Adult Mass	0.893	-5.53E-01	1.62E+00	0.000		0.957	-6.04E-04	4.02E-02	0.334		0.782		-5.50E-03	1.000		0.815		6.24E-03	0.726	
Group Size	0.516		-5.14E-01	0.303		0.673	1.53E-03	-1.03E-01	0.561		0.413	2.29E-03	-5.37E-02	0.013		0.109		2.44E-02	0.000	
Global Range	0.006		2.46E+00	0.000	**	0.291	6.90E-03	-4.95E-01	0.000		0.015		-8.40E-02	0.000	*	0.263		4.54E-02	0.000	
% Grass	0.384		1.65E+01	NA		0.484		-2.59E-01	NA		0.032		-8.07E-01	NA	*	0.032		9.31E-01	NA	*
% Browse	0.011	-6.67E+01	1.81E+02	0.883	*	0.857		-1.56E-01	0.918		0.411		3.92E-01	0.901		0.242		-5.38E-01	0.911	
% Fruit	0.321		1.02E+01	1.000		0.202		2.90E-01	1.000		0.075		3.47E-01	1.000	.	0.409		-2.50E-01	1.000	
Horn/Shoulder Index	0.966		-1.90E-02	0.658		0.463		2.18E-03	0.976		0.071		4.24E-03	0.733	.	0.905	-1.57E-04	6.61E-03	0.947	
Diet Diversity	0.788	-2.70E-01	8.21E-01	0.640		0.329		-3.84E-03	0.980		0.138		-4.77E-03	0.963		0.686	-3.50E-04	1.49E-02	0.949	

*Table 3-5: The best **phylogenetically controlled** linear or quadratic model for the relationship between species trait and optimum climatic variable for species. AP – Annual Precipitation, HT – Hottest Temperature, CT – Coldest Temperature, TR - Temperature Range, AP**p=** Annual Precipitation p-value for the model, AP**coef** and AP^2**coef** - the Annual Precipitation coefficient for the model denoting positive/negative relationship (note where there the AP ^{2} coefficient is present, the best model is quadratic, otherwise linear), AP**ML** – Annual Precipitation Maximum Likelihood (see main text), AP**sig** – Annual Precipitation significance where . (point) <0.1, * <0.05, ** <0.01, *** <0.001.Sample sizes (n) values for each relationship are found in Table 3-6.*

Trait	AP (n=)	HT (n=)	CT (n=)	TR (n=)
Adult Mass	70	59	50	43
Group Size	67	57	48	42
Global Range	71	60	51	44
% Grass	68	57	49	42
% Browse	68	57	49	42
% Fruit	68	57	49	42
Diet Diversity	68	57	49	42
Horn/Shoulder Index	67	57	49	43

Table 3-6: The sample size (n) for the relationships between trait and optimal climatic conditions (AP – Annual Precipitation, HT – Hottest Temperature, CT – Coldest Temperature, TP - Temperature Range) varies due to lack of data (trait) and/or the lack of an optimal climatic condition value. The lack of the climatic value may be due to the variable dropping from the model or the coefficients not resulting in a vertex within the minimum/maximum values for Africa.

Multivariate analysis

The models predicting optimal hottest temperature, temperature range, and global range produced near identical results to the non-controlled results due to lack of phylogenetic signal (see Table 2-3 and maximum likelihood values in Table 3-7).

The relationship between temperature range and percentage of grass in diet indicates that species with little grass in their diet predict areas with small temperature ranges (Figure 3-7 left; $p<0.001$; $R^2=0.439$), and that those species with grass being 70-75% (peak 72.5%) of their diet have the largest temperature ranges. In addition, the mass of species is also important in predicting the temperature range showing a positive linear relationship (i.e. small species have small temperature ranges and the range increases with mass). If only adult mass is included in the model predicting temperature range, the model remains highly significant, but has a lower R^2 ($p<0.001$; $R^2=0.285$).

Global range has a quadratic relationship with annual precipitation (Figure 3-7: Right) with a species' peak global range at 6.69 (804mm) annual precipitation ($p<0.001$; $R^2 = 0.294$). Species with a low optimal annual precipitation have the smallest global range, but there is also a notable fall of global range with very high annual precipitation preferences.

The optimal coldest temperature model contains the same independent variables (linear and quadratic percentage of grass) and similar p and R^2 values to the non-controlled model ($R^2=0.174$; $p=0.001$). The R^2 value suggests a modest strength correlation. Figure 3-6 (Left) demonstrates the quadratic relationship indicating that species with low grass in their diet

have a preference for warmer coldest temperatures, as do the obligate grazers (very high grass percentage). If adult mass is added to the model it remains significant (p=0.01), but has a lower R^2 (R^2 = 0.157), and mass is not significant within the model (p=0.922).

The optimal hottest temperature model has a low R^2 (R^2=0.065; p=0.013) but indicates that species with more grass in their diet have warmer hottest temperature preferences. The low R^2 values for both optimal hottest and coldest conditions suggest that a large proportion of the variation is determined by variables not in the models (Fowler *et al.*, 1998).

The annual precipitation model is significant, but has a lower R^2 value compared to the non-phylogenetically controlled model (R^2=0.081; p=0.02). Percentage of browse is the best predictor of annual precipitation. Figure 3-6 (Right) shows that species with little browse in their diet prefer wetter conditions. However, as above, the low R^2 value suggests there are other factors that affect the annual precipitation preferences or requirements.

Finally, the diet diversity model remains significant compared with the non-controlled result, but without annual precipitation as a variable (R^2=0.216; p=0.003). The model demonstrates that (a) warmer *hottest* temperature preferences contribute to increased diet diversity, (b) warmer *coldest* temperature preferences contribute to reduce diversity, and (c) species experiencing wider temperature ranges have reduced dietary diversity. Multicollinearity was a concern for this model because temperature range is derived from the hottest and coldest temperature variables. Variance inflation factor analysis found that none of the variables had values greater than 10 suggesting that multicollinearity did not affect the results strongly (Kutner *et al.*, 2005).

	Not phylogenetically controlled						Phylogenetically controlled					
Dependent Variable	Model Statistics		Model Variables	estimate	p	sig	Model Statistics		Model Variables	estimate	p	sig
Optimal Hottest Temperature	p	0.025	Grass %	0.0495	0.025	*	p	0.013	Grass %	0.0015	0.034	*
	Adjusted R^2	0.074					Adjusted R^2	0.065				
	n	55					λ ML	0.000				
Optimal Coldest Temperature	P	0.002	Grass % ^2	0.0023	0.043	*	p	0.001	Grass % ^2	0.0032	0.024	*
	Adjusted R^2	0.209	Grass %	-0.2945	0.008	**	Adjusted R^2	0.174	Grass %	-0.3859	0.005	**
	n	50					λ ML	0.603				
Temperature Range	P	1.45E-05	Grass % ^2	-0.0018	0.099	.	P	2.78E-06	Grass % ^2	-0.0018	0.099	.
	Adjusted R^2	0.439	Grass %	0.2677	0.015	*	Adjusted R^2	**0.439**	Grass %	0.2677	0.015	*
	n	42	Adult Mass (Log)	1.8274	0.035	*	λ ML	0.000	Adult Mass (Log)	1.8274	0.035	*
Annual Precipitation (log)	P	8.92E-07	Adult Mass (log) ^2	0.1265	0.040	*	P	0.020	Browse % ^2	0.0003	0.130	
	Adjusted R^2	0.437	Adult Mass (log)	-0.7907	0.101		Adjusted R^2	0.081	Browse %	-0.0394	0.048	*
	n	59	Grass % ^2	0.0004	0.015	*	κ ML	0.741				
			Grass %	-0.0544	0.000	***						
			Browse %	-0.0235	0.000	***						
Global Range (log)	P	7.23E-04	Annual Precipitation ^2	-0.4912	0.007	**	P	1.52E-04	Annual Precipitation ^2	-0.4912	0.007	**
	Adjusted R^2	0.294	Annual Precipitation	6.5757	0.003	**	Adjusted R^2	**0.294**	Annual Precipitation	6.5757	0.003	**
	n	39					λ ML	0.000				
Diet Diversity	P	0.006	Hottest Temperature ^2	0.0004	0.026	*	p	0.003	Hottest Temperature ^2	0.0004	0.038	*
	Adjusted R^2	0.246	Coldest Temperature ^2	-0.0020	0.002	**	Adjusted R^2	0.216	Coldest Temperature ^2	-0.0020	0.002	**
	n	42	Temperature Range ^2	-0.0011	0.002	**	κ ML	0.186	Temperature Range ^2	-0.0009	0.010	*
			Annual Precipitation ^2	-0.0072	0.012	*						

Table 3-7: Best fitting models identifying species traits that predict optimal climatic conditions, diet diversity, and global range for species. StepAIC function used to produce the models before phylogenetic control is applied. When predicting climatic conditions the full model (before stepAIC) contained all species dietary trait variables and log of adult mass including quadratic functions (variable followed by "^2" above). When predicting global range the full model contained all species dietary trait variables, log of adult mass, and optimal climatic conditions including quadratic functions. The full model for diet diversity contained log of adult mass, and optimal climatic conditions including quadratic functions, but not diet to avoid multicollinearity concerns. The phylogenetic models are produced through a custom built forward stepwise selection using the same variables and identifying the optimal model using AIC values. λ and κ ML are the lambda and kappa maximum likelihood value produced by pgls. A λ value of 0 denotes a lack of phylogenetic signature for that variable. Sample size (n) is the same for both result sets. "n" differs due to unavailable values for some species.

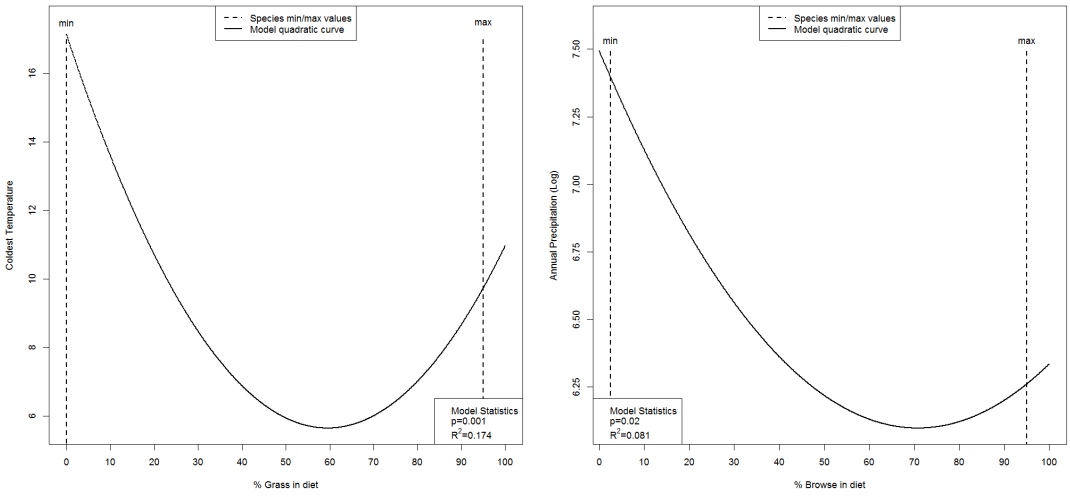

Figure 3-6: Left – The phylogenetically controlled relationship between percentage of grass in species diet and species' optimal coldest temperature. Right – The phylogenetically controlled relationship between percentage of browse in species diet and species' optimal annual precipitation. The minimum and maximum values are for the African species used to build the model.

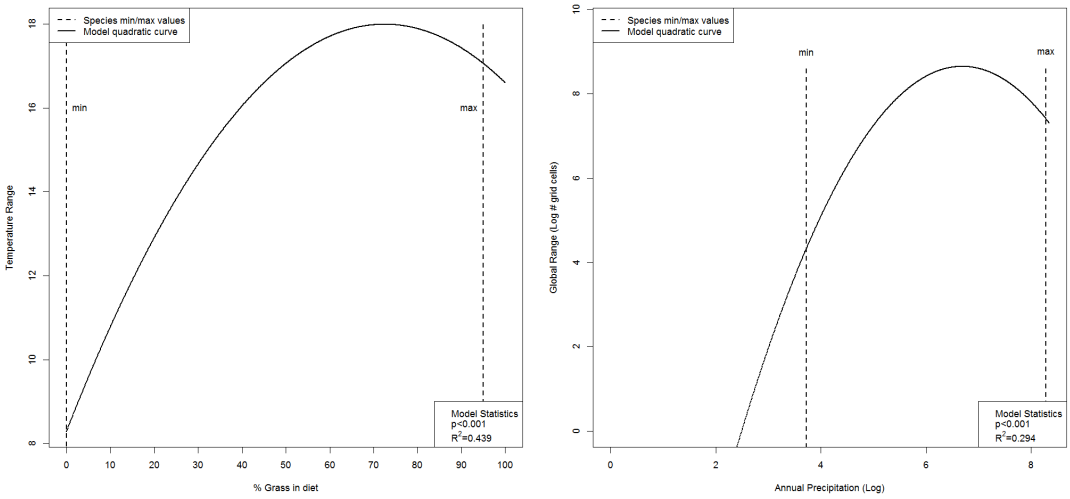

Figure 3-7: Left – The relationship between percentage of grass in species diet and species' temperature range as part of the generalized linear model described in Table 3-7. Right – The relationship between a species' optimal annual precipitation (natural log) and its global range (natural log). The minimum and maximum values are for the African species used to build the model.

Discussion

Identifying the optimal climatic conditions of different species and correlating these to biological traits will aid us in both understanding species current distributions, and predicting distributions in the future. Identifying global range predictors similarly will help pinpoint traits or preferences that may be associated with increased threat in the future.

Temperature range

Temperature range can be predicted by the adult mass and percentage of grass within a species' diet. The relationship with adult mass is a positive linear correlation, whereas the relationship with percentage of grass in the diet is quadratic and better visualized in Figure 3-7 (Left). The relationship between mass and temperature range agrees with our physiological understanding of mammals in general. Larger species, with lower body surface area relative to body volume, are less susceptible to water loss through evaporation. Increased size also offers the potential to store heat during the day by allowing an increase in body temperature which protects against colder conditions overnight. In addition, a greater body temperature reduces the temperature differential to the environment during the day, again reducing water loss (Schmidt-Nielsen, 1990). In studies of camels (*Camelus dromedaries*), periods of drought are associated with greater daily fluctuations in body temperature thereby conserving water (Schmidt-Nielsen *et al.*, 1956). Such great fluctuations are also seen in desert antelope species such as addax and gemsbok (*Oryx gazella*), as well as other large species, such as the eland (*Tragelaphus oryx*; see Estes, 1991). Conversely, smaller species, with a high body surface/volume ratio, see their temperatures rise quicker and have to exploit other strategies such as cutaneous and respiratory evaporation of water (Owen-Smith, 2002; Wilson, 1989). These findings thus support that small species prefer stable conditions which are offered by forests (Cadena *et al.*, 2012; Janzen, 1967) with the larger species being able to accommodate greater fluctuations.

In this way the results provide evidence in support of H_4 where larger body mass enables species to be present in areas with greater fluctuations in temperature. Although the model also includes the percentage of grass within the diet, if the percentage of grass variable is removed from the model it remains highly significant, but with a lower R^2. The inclusion of percentage of grass was not expected; however, grazing species are, on average, larger than browsers and frugivores (Clauss *et al.*, 2008) although not significantly so (Codron *et al.*, 2007). Larger grazers consume high quantities of low quality grass (Codron *et al.*, 2007) found in open savannah areas. These areas are expected to have larger temperature ranges than the forest areas (Cadena *et al.*, 2012; Janzen, 1967) and have more grazing potential than in forests (Bodmer, 1990). The model, therefore, fits with our ecological and physiological knowledge. These findings also suggest that grazing species, especially larger species, may be at reduced risk in the

future given their tendency to tolerate a wider range in temperatures. This suggests a greater flexibility for the future, provided that available grazing habitat remains.

Global range

Global range is predicted by a quadratic relationship with annual precipitation (see Figure 3-7 – right). Global range rises with precipitation up to a peak at approximately 800mm/year, before falling. However, the variability of rainfall across Africa must also be considered. If more area was available with ~800mm/year, then it would follow that the range of species with a preference for these levels would be greater than for those where there was less area available. Table 3-3 shows that this may be the case for species with high rainfall preferences as there is less suitable area available. However, there are large areas of arid conditions that are unutilized by some arid adapted species. This itself is an oversimplified view because the areas are not all contiguous, but it suggests that arid adapted species' ranges are restricted by other factors, for example, human hunting. Uncontrolled hunting has resulted in the addax becoming regionally extinct in Algeria, Egypt, Libya, Sudan, and Western Sahara (Newby & Wacher, 2008; Beudels *et al.*, 2006). The dama gazelle (*Nanger dama*) is no longer found in Libya, Mauritania, Morocco, Nigeria, or Tunisia (Newby *et al.*, 2008; Beudels *et al.*, 2006).

Predicting global range is important because it is negatively correlated with IUCN threat status where a high IUCN value indicates the species is more threatened. IUCN threat status is assigned using a number of criteria including declines in area of occupation or extent of occurrence (IUCN Standards and Petitions Working Group, 2008). If we understand the species traits or climatic conditions that predict global range, and by association IUCN threat, we can better anticipate the impact of future changes, particularly in reference to climatic change. The results indicate that changes in rainfall will likely alter species' global range and therefore threat status. A more arid Africa may mean more suitable habitat for some adapted species, however, there are always limits. At the opposite end of the scale, ranges may contract if precipitation reduces and forests revert to moist savannah. A wetter Africa would have the opposite effect. Whether changes in precipitation would affect those species in the middle precipitation scale to the same degree requires projection modelling (see chapter four). The comments here are an oversimplification as future rainfall changes will vary from area to area. However, the results here indicate that species preferring low or high rainfall are already those at greater risk.

Precipitation

While global range was predicted by annual precipitation, it is interesting to reflect on the fact that there was no strong model for predicting optimal precipitation of species when phylogenetic control was applied. Table 3-7 provides the "best" model with a low R^2 of 0.081. From previous research rainfall has often been identified as an important variable influencing antelope distribution (Chirima *et al.*, 2013), demography (Owen-Smith, 1990), biomass (East, 1984), and population dynamics (Ogutu & Owen-Smith, 2003; Owen-Smith, 2002). It would have proven interesting to uncover species traits that predict different levels of rainfall. The non-phylogenetically controlled results indicate that three variables affect precipitation within species ranges. The first variable, a negative relationship with percentage of browse, indicates less rainfall is required by species with high browse in the diet. The second variable is a quadratic function of percentage of grass which also represents a negative relationship. Finally, the body mass quadratic function produces a curve where very small species require high rainfall, this falls to a nadir of species weighing approximately 20kg before rising. Therefore, species with very low body mass, low browse, and low grass in their diet have higher precipitation values. This suggests a correlation, albeit not in the model, between high fruit in the diet and high rainfall as predicted (P_3). However, this result is not phylogenetically controlled and must be treated cautiously. The results suggest that there are no simple rules defining rainfall requirements and that multiple strategies have evolved to enable species to succeed in all precipitation bands.

It was also predicted that precipitation as an independent variable would demonstrate negative correlations with (a) body mass and (b) shoulder/horn length ratio (P_4). However, neither of the relationships were found to be significant whether or not phylogeny was controlled for. This is surprising considering previous research suggests selection for small body size for manoeuvrability in dense habitats (Bro-Jørgensen, 2008) which are predicted by high rainfall (Whittaker, 1975). Previous work has suggested that horns of antelopes tend to be both sloped (Estes, 1991), and smaller (Janis, 1982) for manoeuvrability in forest species, but the result was not found here. This again may be due to the high variability of body mass and shoulder/horn ratio throughout the optimal precipitation range. This variability is demonstrated by the relatively small arid-adapted dik-diks, and by the larger species found in the forests such as the sitatunga, which has highly adapted hoofs for swampy forest habitats, and is commonly found foraging in deep water (Stuart & Stuart, 2000; Estes, 1991). H_4 is rejected as no pattern exists across the

entire range. This adds to the evidence that antelope species fill multiple ecological niches across a range of climatic conditions.

Diet diversity

No single climate variable predicted diet diversity (Table 3-5). The multivariate correlations revealed that diet diversity is dependent on four climatic variables, including the quadratic function of annual precipitation that predicted a general fall in diet diversity (i.e. more specialist feeders) with increased rainfall. This partially supports H_1 which posited specialist feeders would be found at either end of the precipitation scale. However, the relationship also shows that generalist species are found in areas with low rainfall which was not expected. This is likely related to the need for arid adapted species to be flexible in their diet where vegetation is sparse. However, when phylogeny is controlled for, optimal annual precipitation is removed from the model. Also, the bivariate models found no relationship between diet diversity and precipitation, and therefore the hypothesis cannot be supported by these findings. Dietary specialists (i.e. with low diversity index values) and generalists (high values) are therefore found across the annual precipitation gradient and points to a dietary heterogeneity amongst species.

The phylogenetically controlled diet diversity model includes quadratic functions for optimal coldest and hottest temperatures, and temperature range using a multivariate model. The model demonstrates a complex relationship where (a) hotter hottest temperature preferences contribute to increased diet diversity, (b) warmer coldest temperature preferences contribute to reduced diet diversity, and (c) species experiencing wider temperature ranges have reduced dietary diversity. The strongest influence on the model comes from the optimal coldest temperature variable where species with a preference for warmer coldest temperatures, such as found in low latitude tropical forests, have a more selective diet. This selectivity agrees with previous reports of antelope feeding styles by forest species (Estes, 1991; Jarman, 1974), where those found in colder conditions were less selective. In general, and when all model variables are combined, species with preferences for warmer coldest and warmer hottest conditions will have a lower diet diversity than those preferring cooler conditions if the temperature range is the same (see Figure 3-8). At lower temperatures, species with a smaller temperature range are predicted to have a greater diet diversity than those with a larger temperature range, but there are no species that fit these criteria. Species with cooler coldest optimal temperatures typically have larger temperature ranges (>30°C)

and in these species the diet diversity is higher. The trend towards lower diet diversity in warmer conditions is due to the strength of the coldest temperature variable and results in a general trend where species found in warmer, less variable conditions (e.g. tropical forest areas) have a lower diet diversity.

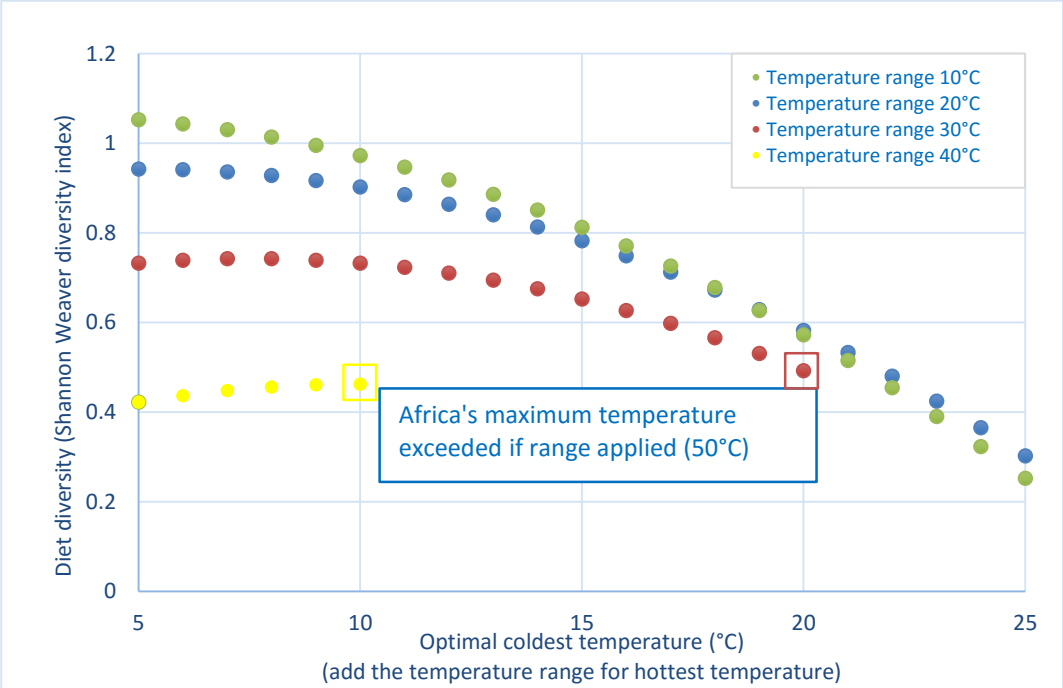

Figure 3-8: Diet diversity predicted by the model (see main text) for constant temperature range values. For example, for the "temperature range 10°C" series, at 5°C optimal coldest temperature (x-axis) the optimal hottest temperature would be 15°C. There are no antelope species with low optimal coldest temperatures and small temperature ranges. Therefore, the general trend is that species with large and small temperature ranges have reduced diet diversity.

Coldest temperature

Percentage of grass in a species' diet predicts the optimal coldest temperature exhibited by a species. In contrast to the relationship with temperature range, Figure 3-6 (Left) shows that with increasing grass in the diet, up to ~60%, there is a fall in the optimal coldest temperature. The temperature then rises as grass content approaches 100%. This mirrors the temperature range relationship in many ways. Tropical forests have high mean temperatures (Whittaker, 1975) and small temperature ranges (Cadena *et al.*, 2012; Janzen, 1967) indicating warmer coldest temperatures. Those species with low grass in their diet tend to be dense forest species where there is little grass available (Bodmer, 1990). In addition, selective feeders are generally smaller than unselective feeders (Jarman, 1974) and do not include the largest antelope species. Obligate grazers (>90% of grass in their diet) are therefore slightly lower in mass and potentially less well

adapted to cold conditions (see above) than larger bulk grazers. This could explain the optimal coldest temperature rising with higher levels of grass in the diet. This also suggests that larger species with a more varied diet have the lowest optimal coldest conditions. However, adding mass to the model results in a poorer fitting model, and mass is not significant. With only modest R^2 scores it is therefore likely that other factors influence coldest optimal temperature. The percentage of grass in antelope species diets contributes to their ability to tolerate colder conditions and indicates species that may be better adapted should the climate become cooler; however, this is an unlikely scenario as climate predictions project rising temperatures (IPCC, 2013b).

Models and model performance

The validity of the approach taken here is strongly supported by a mean AUC values of 0.958 for the models, and the fact that models of only four from seventy-four species were not classed as having "High usefulness" (Swets, 1988). The models in the present study fall into the "Bioclimatic envelope models" designation, according to Araújo and Peterson's (2012) descriptions of models and their variables. However, the simple envelope model paradigm was extended to incorporate a human footprint filter (Thuiller *et al.*, 2006a), thereby accounting for the fact that humans negatively impact antelope distributions through disturbance (Singh *et al.*, 2010). This reduces the likelihood of species presence in locations heavily affected by humans such as urban areas.

Understanding which models perform better than others helps establish confidence levels in the models. The AUC scores and usefulness categories produced by Swets (1988) are often referred to, but other authors use different categories based around Swets work (Araújo *et al.*, 2005; Thuiller *et al.*, 2003). The characteristics of a species' distribution that result in higher AUC scores has also been reviewed. Ashcroft *et al.* (2011) demonstrated, using plant species, that clustered distributions produced the highest values, as did those with small distributions. The worst performing species were those with large distributions across multiple habitat types. Others have advocated that these species characteristics should also be incorporated when evaluating model performance (Guisan *et al.*, 2007).

In this study the antelope species with AUC scores less than 0.9 have little in common morphologically or ecologically, but it is still important to understand what variables might affect accuracy of the models; confidence in the results and future predictions based on the models relies upon this. After investigation a clear relationship between the fragmentation of a species' range and a poorer fitting model (lower AUC) was found. This clearly disagrees

with Ashcroft *et al.* (2011) who found the opposite. Guisan *et al.* (2007) suggest understanding of the individual species' characteristics may prove important in further understanding the low scores. The results here relate to very different species to Ashcroft *et al*. (i.e. mammals versus plants), and therefore different reasons for fragmentation need to be considered. I suggest the history of the species should be considered where possible. It may be that being a heavily hunted species results in fragmentation rather than other factors such as climate, habitat, or interspecific interactions. If detailed information was available it could be used to better improve the model performance, or to act as weighted filters as with the land transformation data.

The differences in the persistence of species within refugia through past climatic episodes is another cause of fragmentation in antelope distributions (Lorenzen *et al.*, 2010) that may impact on model performance. For example, the hartebeest has been affected by past climatic events which have resulted in seven subspecies being recognized (Flagstad *et al.*, 2001; see Figure 3-9). The western clade and eastern clade are thought to have formed due to isolation either side of an expanding rainforest belt ~400,000 years BP. Approximately 200,000 years BP, further diversification occurred within the southern and eastern clades resulting in the current subspecies. Both of these diversification events are considered to be related to climate change (Flagstad *et al.*, 2001). The different subspecies have adapted to their new climates. For example, body size is positively correlated to rainfall, with *A. b. major* larger than the eastern clade subspecies (Capellini & Gosling, 2007). In addition, Lichtenstein's hartebeest (*A. b. lichtensteinii*) has adapted to woodland areas, whereas the others have adapted to savannahs (Flagstad *et al.*, 2001). Conceivably, these regional adaptations could impact on model performance. Each fragmented subspecies appears to have a distinct climatic niche, but there may be overlap between other subspecies. When all subspecies are grouped at a species level, the climatic niche breadth would be wider than for any one subspecies, and this would be represented by the model. Therefore, there may be suitable climatic conditions (or habitat) that are connected to one subspecies' distribution, but are considered suitable only for a different subspecies, and are therefore inaccessible by the adjacent subspecies (for example, woodland habitat). The models would predict these areas as suitable, but the species would not be present. The impact on the models would be reduced specificity due to an increase in the number of false positives predicted. It is unclear to what degree this method of fragmentation affects the models. The hartebeest model which has the second lowest AUC value of those assessed, provides some evidence, but the impact from this form of fragmentation requires further study.

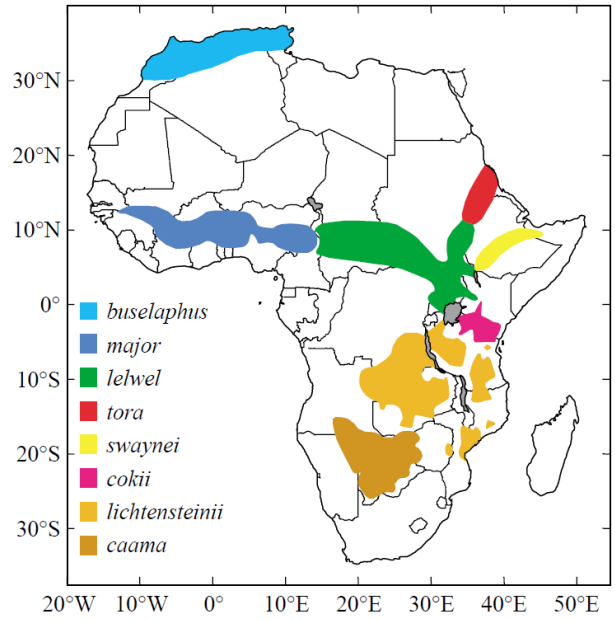

Figure 3-9: General historic distributions of recent hartebeest subspecies including the extinct Alcelaphus buselaphus buselaphus *(from Flagstad et al., 2001). Three clades are considered by Flagstad et al. (2001): The western clade (*A. b. buselaphus *and* A. b. major*), eastern clade (*A. b. lelwel, A. b. tora, A. b. swaynei*, and* A. b. cokii*), and the southern clade (*A. b. lichtensteinii *and* A. b. caama*).*

The relationship between the models' AUC scores and range size is significant, albeit with a weak to modest correlation (R^2= 0.194; see Figure 3-2 right). The African buffalo, hartebeest, and topi have the lowest AUC values and are towards the upper end of the range sizes. This partially agrees with Ashcroft *et al.* (2011) where he found a relationship between widespread species encompassing multiple habitat types and lower AUC. However, the results here suggest a quadratic relationship whereby species with small ranges also deliver poor AUC scores. This is contrary to Ashcroft *et al's* findings where they suggest rare species had high AUC scores. However, the history and threats to the species need to be considered here because there are different reasons for rarity. A species may be specialist and rare, but equally it may be rare due to human based threats. For example, the worst performing model, for the extinct in the wild scimitar-horned oryx, was based on a limited and fragmented distribution (Figure 3-10). The current range of the scimitar-horned oryx is significantly different to the 1990 range suggested by East (1990; see Figure 3-10 inset left) which was already considered greatly reduced. The model for this species is based on the fenced reintroduction sites (Figure 3-10 main image) where the scimitar-horned oryx is now managed (IUCN SSC Antelope Specialist Group, 2013). These sites are in safe areas, which are believed to be historically indigenous, but are still very limited. The cause of the decline of scimitar-horned oryx is linked to overhunting, and habitat loss related to domestic livestock, i.e. not climate related. This suggests a far wider area would be climatically suitable

and populated by the species if these influences had not caused its extirpation. The result of this is a model that represents the climate in the reintroduction sites, but because that also represents a far wider climate, the sensitivity of the model would be low, resulting in the poor model (Figure 3-10 inset-right).

In summary, the analysis of the models suggests that large ranged species with fragmented ranges should be regarded with a level of caution, as should those with limited ranges, and we should pay attention to species histories.

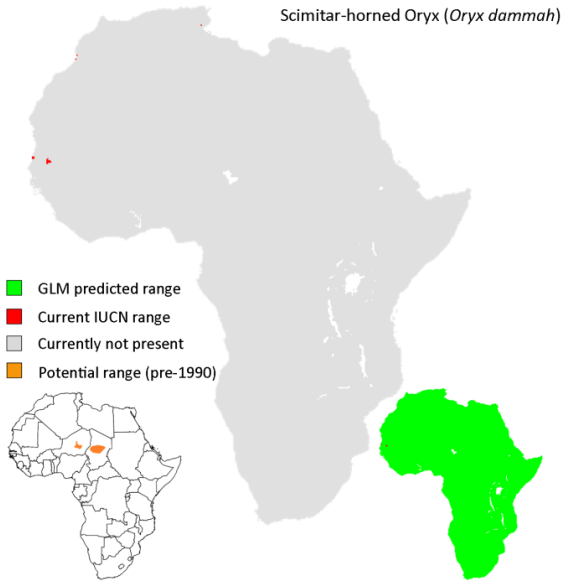

*Figure 3-10: Current and GLM prediction (inset right) of Scimitar-horned oryx (*Oryx dammah*). Inset image (left) 'possible' range during a pre-1990 study (East, 1990).*

Species diversity and heterogeneity

Greater antelope species diversity was found in areas with rainfall approximately 1,000mm/year. This supports, in part, H_2 that greater species diversity should be found in areas with high habitat heterogeneity, determined by rainfall, that provide the widest selection of dietary options. It was predicted that this would occur in open savannah areas with rainfall of approximately 1,000 mm/year linked with previous findings of greater biomass under these conditions (East, 1984), a greater habitat heterogeneity (du Toit & Cummings, 1999), and greater primary productivity available to antelopes (Jarman, 1974). H_2 also hypothesized that the reason behind the greater antelope diversity was multiple foraging options and strategies. Table 3-2 details the trend towards a more equal spread of species diets expressed in the mid precipitation areas compared to the very high rainfall

areas. This is not seen in comparisons between low and mid precipitation areas. These differences combined with Figure 3-4 provide support towards H_2, but the evidence is not conclusive. Further research into plant diversity is required to confirm a direct relationship to habitat heterogeneity. However, greater antelope diversity, and a more equal spread of diet types found in species in areas with precipitation between 500 and 1,500mm/year, suggests greater diversity in the forage available.

The precipitation at which antelope species diversity peaks is low compared to that of 2,000mm/year found in primates (Kay *et al.*, 1997). This is likely due to the terrestrial nature of antelopes rather than arboreal primates. Jarman (1974) indicated a lack of primary productivity available to antelopes in forests (and deserts). Bodmer (1990) describes that, while primary productivity is high in forests, forage may not be abundant enough to support grazers or browser-grazers. The results here largely agree with those findings; I found that frugivorous and browser species are increasingly prominent in wetter areas, but species richness declines in those areas. This, accompanied by the physical complexities of large species' movement in forests indicated by the manoeuvrability hypothesis (Bro-Jørgensen, 2008), may contribute to fewer species in the forest/high precipitation areas compared with more heterogeneous habitats.

The analysis of diet type at varying levels of precipitation (Table 3-2) provides the supporting evidence for H_3 that frugivore species are largely restricted to forest areas associated with high rainfall where fruit is more abundant. Here, I found that frugivores dominate (>50%) in areas above 1,500mm annual precipitation, where the habitat becomes dominated by forests. This is accompanied by a reduction in grazers of all types, although variable grazers retain a percentage in all precipitation subdivisions. Browsers are evenly distributed between all areas. The results here do not take into account the area of the precipitation subdivisions, nor the fact that there is not an equal distribution of species in each foraging class, but the results demonstrate the different diet specializations in each subdivision. The results here support the findings of Bodmer (1990) who identified greater frugivory in forests, and that this is related to high rainfall (P_3). Still, the percentage of fruit does not have a positive relationship with optimal precipitation when phylogenetically controlled, although it is highly significant without. There is no relationship between fruit in the diet and temperature range, although this too is significant without the phylogenetic control. The high impact of the phylogenetic control is likely due to the fact that frugivory is concentrated within the speciose group of duikers (see *Cephalophus* and *Philantomba* genus' in Figure 2-4

right), and lack of statistical power may explain why H_3 cannot be supported based on the controlled results.

Generalist species were not commonly found in areas with precipitation >1,500mm/year. This may not be the *a priori* assumption as generalist species might be considered adaptable for all conditions due to their ability to forage on all vegetation types. However, from the results (Table 3-2) it is clear that while they make up a high proportion of species found in arid areas, they are not commonly found in forest areas. The reason for this may lie in the requirement to be an adaptable forager in harsh arid areas where forage may vary spatially and temporally due to inconsistent rainfall, and is sparsely distributed (Rubinstein, 1989). Under these conditions flexibility to forage on whatever resources are available may outweigh specificity.

One of the reasons this study was conducted on antelopes was because of the diverse nature of the taxon. African antelopes have evolved to fill many niches across a highly heterogeneous landscape, and the diversity in their adaptations may explain why simple rules predicting optimal climatic conditions proved elusive in the present study. An example of this is body mass; it was hypothesized that smaller species would require high rainfall which in turn produces the forests and fruit required. However, several larger species, such as the bongo (*Tragelaphus eurycerus*), forest buffalo (*Syncerus caffer nanus*), and previously mentioned sitatunga are present in forests and swamp areas (Stuart & Stuart, 2000; Estes, 1991). Equally, there are small antelopes, such as dorcas gazelle (*Gazella dorcas*), and the dik-diks, that live in more arid climates (Estes, 1991; Maloiy, 1973).

Africa is a diverse continent in terms of climate and the habitats determined by it. Each of these habitats plays host to a heterogeneous range of antelope species with differing morphology and ecology. Millions of years of evolution have enabled species to evolve adaptations filling many ecological niches. This was indirectly presented by Pienaar (1974) who produced a table showing optimal habitats (Table 1 - Pienaar, 1974). In addition Pienaar highlighted that while some species are tied closely to specific habitats, the adaptability of some species, such as the impala (*Aepyceros melampus*), enable them to exploit multiple habitats. Unfortunately no analysis of species traits were made, but the findings offer support to those found here. Antelopes of varying size and diet have evolved to fill many niches in all habitats, even at the extreme ends of Africa's diverse climate. Furthermore, it is likely that the climatic history of Africa has influenced the overall diversity of antelopes. Past climatic events have caused rapid contraction and expansion of habitats that have

driven high inter- and intra-specific diversity, particularly in the highly diverse East African region (Lorenzen *et al.*, 2012).

This study has identified relationships binding species traits to climatic conditions. Although the significance reduced when phylogenetic control was applied, through multivariate analysis it is clear that variables interact to predict species traits and optimal conditions for antelope species. The species diversity model presented here highlights the importance of annual precipitation in predicting species richness. Equally, the other climatic variables were significant in describing the diversity of a species' diet. The relationships between species traits and optimal climatic conditions described above also offer new avenues for further research and aid in our understanding of this diverse and important group of animals.

Appendix

		No phylogenetic control				Phylogenetic control applied			
Climate Variable	Species Trait	Linear Model p value	Linear Model R^2	Quadratic Model p value	Quadratic Model R^2	Linear Model p value	Linear Model R^2	Quadratic Model p value	Quadratic Model R^2
Optimal Hottest Temperature	Mass Adult (Log)	0.0878	0.0486	0.2310	0.0493	0.9963	0.0001	0.9575	0.0036
	Group Size (Log)	0.0707	0.0552	0.1698	0.0603	0.9990	0.0000	0.6733	0.0184
	Global Range (Log)	0.3827	0.0127	0.2813	0.0421	0.4735	0.0127	0.2914	0.0421
	% Grass	0.0367	0.0744	0.0749	0.0884	0.4841	0.0031	NA	0.0000
	% Browse	0.0569	0.0622	0.1657	0.0622	0.8566	0.0027	0.9517	0.0040
	% Fruit	0.5603	0.0060	0.4812	0.0258	0.2018	0.0286	0.2144	0.0530
	Horn/Shoulder Index	0.0338	0.0753	0.0980	0.0783	0.4628	0.0135	0.7591	0.0138
	Diet Diversity	0.1927	0.0296	0.4275	0.0299	0.3289	0.0195	0.6209	0.0208
Optimal Coldest Temperature	Mass Adult (Log)	0.0151	0.1045	0.0109	0.1567	0.7818	0.0046	0.9403	0.0051
	Group Size (Log)	0.0296	0.0894	0.0787	0.0967	0.4938	0.0141	0.4132	0.0382
	Global Range (Log)	0.0391	0.0751	0.0784	0.0900	0.0146	0.0781	0.0527	0.0935
	% Grass	0.0003	0.2226	0.0009	0.2356	0.0318	0.0096	NA	0.0000
	% Browse	0.5982	0.0053	0.8692	0.0054	0.4113	0.0171	0.6447	0.0214
	% Fruit	0.0002	0.2279	0.0006	0.2479	0.0752	0.0497	0.2200	0.0563
	Horn/Shoulder Index	0.2129	0.0297	0.0308	0.1276	0.0705	0.0519	0.0721	0.0901
	Diet Diversity	0.7916	0.0013	0.1410	0.0726	0.1382	0.0373	0.1432	0.0677
Temperature Range	Mass Adult (Log)	0.0003	0.2548	0.0015	0.2609	0.8154	0.0047	0.9211	0.0077
	Group Size (Log)	0.0005	0.2466	0.0019	0.2575	0.1094	0.0526	0.2976	0.0583
	Global Range (Log)	0.2592	0.0282	0.3321	0.0489	0.2635	0.0303	0.3314	0.0517
	% Grass	0.0000	0.3999	0.0000	0.4413	0.0322	0.0108	NA	0.0000
	% Browse	0.0737	0.0725	0.1319	0.0920	0.2418	0.0330	0.5300	0.0344
	% Fruit	0.0010	0.2247	0.0036	0.2346	0.4094	0.0213	0.5431	0.0341
	Horn/Shoulder Index	0.0018	0.1999	0.0083	0.1999	0.9169	0.0020	0.9047	0.0088
	Diet Diversity	0.6502	0.0048	0.3327	0.0511	0.7463	0.0068	0.6860	0.0231
Annual Precipitation	Mass Adult (Log)	0.7762	0.0013	0.8611	0.0047	0.9963	0.0001	0.8934	0.0067
	Group Size (Log)	0.0726	0.0519	0.0604	0.0893	0.5161	0.0110	0.7323	0.0144
	Global Range (Log)	0.0208	0.0795	0.0665	0.0812	0.0060	0.0798	0.0470	0.0817
	% Grass	0.5150	0.0069	0.6410	0.0145	0.384	0.0128	NA	0.0000
	% Browse	0.0033	0.1312	0.0019	0.1860	0.0283	0.0584	0.0111	0.1168
	% Fruit	0.0042	0.1444	0.0035	0.1721	0.3206	0.0186	0.4558	0.0285
	Horn/Shoulder Index	0.1357	0.0355	0.2211	0.0483	0.9665	0.0006	0.9961	0.0007
	Diet Diversity	0.1109	0.0405	0.2601	0.0432	0.8587	0.0025	0.7878	0.0116

Appendix 3-1: Full p and R2 values for the models presented in Table 3.4 and Table 3.5.

4. Ensemble forecasting predicts large range contractions for Africa's already threatened antelope species

Abstract

Global biodiversity is under threat from multiple fronts. The Millennium Ecosystem Assessment predicts that climate change (CC) will be the "dominant direct driver of biodiversity loss" by the end of the 21st century and shows a trend for a "very rapid increase in the impact" of CC on those ecosystems, and there is already growing evidence of species being affected by CC. Africa is an area of high climate variability and high vulnerability to CC. Climate projections suggest average temperatures could rise by 3-4°C before the end of the century, further influencing species distributions and suitable climate areas.

In this study I present ensemble forecasts, incorporating three climate models for three climate scenarios. I predict the future distributions of 73 African antelope species using three approaches. The first is a pessimistic representation of species distributions in a future where they are unable to disperse from their current range to track CC. The second, optimistic approach, permits species to disperse at a given rate based on body mass. Finally, the envelope approach presents a comparison of suitable climatic conditions between now and the end of the century that are connected to the existing distribution over time (i.e. not restricted by current distribution or dispersal). These three approaches are respectively representative of (a) a future where continuing human pressure restricts natural dispersal, (b) a conservation friendly future where human pressures are removed, and (c) the potential of species if human pressures and dispersal were not restrictive. The predictions indicate that 81-85% of species (59-62 of 73) will exhibit a contraction in range based suitable climate, and that the average contraction of those species is 39.4-50.1%. Up to six of 73 species are predicted to be without any climatically suitable areas in 2080 depending on the modelling and forecasting approach taken. These include the hirola (*Beatragus hunteri*) that has no suitable areas under any approach. Worryingly, there is also a disproportionate reduction in the predicted distribution of threatened antelopes, whereas species with a broader climatic niche and a preference for warmer temperatures perform better.

Introduction

The Earth is experiencing a period where the species extinction rate is higher than the background rate (Barnosky *et al.*, 2011) and could, if it continues, be the next mass extinction. The current episode of extinctions is unique in that it is the first time a species has had a major impact on the extinction risk of others. Species are threatened by fragmentation and loss of habitat, competition from non-native species and livestock, increasing pollution and spread of pathogens, over-exploitation, and climatic change (Barnosky *et al.*, 2011; UNEP, 2010; MEA, 2005). While all are serious threats, it is climate change (CC) that some consider will be the dominant threat to biodiversity by the end of the 21st century (MEA, 2005). Current climate change is caused by rising greenhouse gas (GHG) levels (including CO_2), and is influenced by human activities (IPCC, 2013b; 2007). However, changing levels of CO_2 links current climatic conditions with the recent mass extinctions (see Barnosky, *et al*., 2011).

CC affects areas differently around the globe and at regional and local scales. Africa is an area of high climate variability and high vulnerability to CC. Africa's vulnerabilities to CC have been divided into economic, agricultural, water stress, human health, and ecosystem change (Yousuf, 2010; Boko, *et al.*, 2007). Research on Africa's climate includes work on past, present and future climatic conditions (Spinage, 2012; Hulme *et al.*, 2005; Tadcross *et al.*, 2005; Hulme *et al.*, 2001). However, Africa is an area where large degrees of uncertainty apply to the climate predictions (Boko *et al.*, 2007). This uncertainty is largely due to the difficulties of modelling El Niño/Southern Oscillation (ENSO) and land cover changes, that strongly affect Africa's climate (Hulme *et al.*, 2005). For example, temperature predictions include an alarming rise of 7-9°C under a fossil fuel intensive scenario (A1F climate scenario), and by 3-4°C under a more balanced fuel scenario (A1B climate scenario), for the period 2080-2099 (Boko *et al.*, 2007). Predictions of precipitation are particularly uncertain due to the complexities in modelling mechanisms such as the hydrological cycle, orographic precipitation, sea-surface temperature anomalies, deforestation, and soil moisture (Boko *et al.*, 2007). An example of this is the Sahel region, an area that has experienced large reductions in rainfall since 1950 (Odada & Olago, 2005), and presents unique modelling problems. Thus, different organizations' Atmosphere-Ocean Global Circulation Models (AOGCMs) offer a range of future forecasts including both significant wetting and drying for the area. Uncertainty is also found in the tropical zone of Africa with some AOGCMs predicting drying in the west, while others suggest wetting, but most agreeing that increased

precipitation will be seen in the east of this area (Malhi *et al.*, 2013). For other areas general consensus on climate trends exists. Drying is expected along the Mediterranean coast and northern Sahara along with southern Africa during the winter (Boko *et al.*, 2007).

CC affects biodiversity at multiple levels from individuals to biomes. However, this study focuses at the species level and the impact of CC on the distribution of Africa's antelopes. The threat of CC may be unique in its ability to impact all species. Since the 1800s scientists have demonstrated that species distributions are strongly linked to climate, and therefore any change in climate will have an impact on those species (Quintero & Wiens, 2013; Araújo & Peterson, 2012; Whittaker, 1975; Pienaar, 1974; Janzen, 1967; Grinnell, 1924; Von Humboldt & Bonpland, 1805). Understanding climatic tolerances and preferences of species (their climate envelope) provides insight into species distributions and helps us predict their sensitivity to CC (Thuiller *et al.*, 2005a). Furthermore, modelling current and future species distributions can help us assess the impacts of the other threats. Species distribution models (SDMs), including climate envelope models (CEMs), are empirical models that correlate environmental predictors with species observations in the field. These models can then be used to predict the distributions of species based on future climate forecasts (Guisan & Thuiller, 2005). Modelling above the species level (e.g. communities or ecosystems) is highly complex as it relies on interacting processes between multiple species, their dependency on future human activity, and stochastic events. If all these projections were possible and linked with further predictions of climate change, the resulting models would have high levels of uncertainty (Evans, 2011). Given this complexity, many have taken the approach of modelling individual species, or groups of species, and incorporating additional species characteristics, such as dispersal, where possible.

African antelopes are a highly diverse and speciose group. With 63% of species populations declining and 23% listed as threatened by the IUCN, conservation measures are already required. Antelopes play critical roles in the ecosystem by moulding landscapes, as seed dispersers, nutrient recyclers, and as prey species. They are also a vital source of protein for indigenous human populations. Antelopes also differ greatly in terms of habitat and foraging preferences, social grouping, size, and sexual dimorphism (Estes, 1991), and thus provide a suitably diverse group to investigate morphological and ecological trait correlations with the impact of CC. Gaining an understanding of which species prosper or suffer, and how their distributions shift due to the changing climate, are important building blocks for developing conservation strategies.

The use of climatic variables to understand antelope distributions has sound backing in literature. Precipitation is widely considered as important to antelope species distribution (Chirima *et al.*, 2012; Hopcraft *et al.*, 2012; Hopcraft *et al.*, 2009; Evangelista *et al.*, 2008; East, 1984) and significant in the density and survival of populations (Owen-Smith *et al.*, 2012; Owen-Smith, 1990;). Also, temperature has been identified as important for understanding distribution (Chirima *et al.*, 2012; Evangelista *et al.*, 2008). Here I use precipitation and temperature as predictors and produce forecasts of species distributions including three climate scenarios, incorporating three AOGCMs, in three novel approaches to identify species at risk, and those that will prosper.

There are criticisms aimed at SDMs and similar modelling techniques. These include poor choice of predictors and modelling techniques, excluding ecological theory that underpins species distributions, and faults in selection of scale (Fordham *et al.*, 2012; Austin & Van Niel, 2011; Elith & Leathwick, 2009). It is important to recognize these criticisms and address them where possible. Here I completed a rigorous variable assessment (see chapter three) before selecting my predictors. The selected variables are both the best predictors, based on the model performance, and are also recognized in literature as being ecologically important for the antelope species. The models, based on quadratic generalized linear models (GLM), also allowed the optimal temperature and precipitation conditions for each species to be calculated. These were used to investigate relationships between the predicted change in range size and species ecological, morphological, and other species trait data such as IUCN threat status. Finally, the models and predictions are based on a spatial scale of 10' grid cells (approximately 344km^2). The selection of 10' grid cells reflects the scale above which, as they became too coarse, GLM SDMs were found to fall in performance (Seo *et al.*, 2009). Also, climate predictions are largely the result of interpolation between widely dispersed data points that represent meteorological stations (Hijmans *et al.*, 2005). This being the case, fine scale predictions are likely a result of greater levels of smoothing between points rather than having additional data between those points.

SDMs and CEMs do not, by default, include dispersal when considering species distributions in the future (Travis *et al.*, 2013; Araújo & Peterson, 2012) and this has been considered a component of modelling that requires development (Thuiller *et al.*, 2008). Dispersal itself varies between species and relies on many factors. There has been little study on the dispersal velocity of African antelopes and ungulates in general (but see Haanes, *et al*., 2011; Apio, *et al*., 2010; Mockrin, 2009; Matson, *et al*., 2006). Most research is confined to

migratory species and focusing on range fidelity (Morrison & Bolger, 2012). The study of species dispersal is complex and many factors influence dispersal velocity at the individual or population level. Natal dispersal may differ by age, sex, population density and structure, resources, competition, management, climate (including CC), and inbreeding avoidance (Prévot & Licoppe, 2013). It is important to include some measure of dispersal when predicting a species' future range. Often SDMs, and any predictions based on them, ignore this aspect of biology simply allowing species to freely disperse. This results in species demonstrating unrealistic range shifts (Thuiller *et al.*, 2006a). Due to limited information being available on species specific dispersal velocities for antelopes, I estimate dispersal velocity for all species based on Schloss *et al*.'s (2012) equation linked to body mass. Each species is then limited to a maximum dispersal range based on that estimate. From previous studies it was suggested that their relatively large size would place antelopes at low risk from being unable to keep pace with climate change (Schloss *et al.*, 2012). However, the wide range of body mass exhibited by this group offers the chance to investigate this further. With dispersal based on body mass, it suggests the largest of the species should be able to track changes in climate with greater ease than the smallest, thus placing the small species at greater risk.

Dispersal can be restricted by other barriers. Antelopes fall into one of a number of feeding types with some species being specialist browsers, grazers, or frugivores (Gagnon & Chew, 2000; Jarman, 1974;). It is therefore possible that unfavourable habitat, for example, grassland for forest dwelling frugivores, would present a potential barrier for dispersal as has been witnessed through human driven habitat fragmentation (Lehman *et al.*, 2006; Zhang & Usher, 1991). To establish if this presents a concern for antelopes each species is assigned a habitat restriction: open (grassland/savannah), closed (forest), or both (generalist). When modelling dispersal, the open and closed specialists are restricted from crossing unfavourable habitat, and all species are unable to traverse human dominated areas. These results are then compared to results where habitat is not a limiting factor.

I present three approaches based on different assumptions about dispersal. The first is a measure of the expansion or contraction of range based on the suitable climate for the species, not the species' actual distribution. Based on the species' climate envelope, this gains an understanding of the change in suitable conditions for a species if it was unaffected by humans or other barriers such as dispersal. The second approach is a pessimistic approach where species are unable to disperse beyond their current range. The final approach is an

optimistic approach where a species are able to disperse from their current distribution, limited by dispersal velocity, and exploit new suitable areas. For the two scenarios that allow dispersal, a species' range must also be connected through time to allow species to reach previously unoccupied areas. Here I predict the antelope ranges for three time periods (2030, 2055, and 2080). This removes the possibility of the model suggesting areas far removed from the actual distribution.

Due to the climate in Africa being difficult to predict (Boko, *et al*., 2007), and differences found in AOGCM climate predictions for the continent, ensemble modelling was developed for this project to incorporate multiple AOGCMs. For each species three distribution projections were created based on climate projections from different AOGCMs. The three projected distributions are then combined to create an ensemble model where overlapping predictions provide greater confidence of suitable conditions. This is then replicated for three different climate scenarios that offer alternative climatic futures (IPCC, 2007).

Finally, humans negatively impact antelope distributions through disturbance (Singh *et al.*, 2010). For this reason a land transformation weighted filter was applied (Thuiller *et al.*, 2006a) to the models to exclude species from areas which were climatically suitable, but due to a high human footprint would preclude species presence.

SDM predictions are an important conservation tool (Worthington *et al.*, 2014; Lawler *et al.*, 2011). They facilitate our understanding of range change to identify species at risk (Thuiller *et al.*, 2006a). To expand on this I investigate changes in a range size to species traits. This enables us to identify not just species, but species traits, that signify cause for conservation concern. For example, as noted above, body mass may limit dispersal for small species. In addition, habitat fidelity towards open or closed areas may limit the potential to track climatic change. Partly linked with this, habitat specialists are expected to be dietary specialists being obligate grazers, browsers, or frugivores. To investigate dietary specialism a diet diversity index, based on the proportion of grass, browse, and fruit in the diet, was assessed against change in range.

Understanding future distributions of species and any traits that make those species more at risk than others can help produce the blueprint for conservation strategy for the next century. Ensuring the conservation of antelopes would furthermore help protect other species and ecosystems due to their central role across the trophic levels. To lose such species could lead to catastrophic trophic cascade affecting humans and environment alike.

Predictions

The general effect of CC and rising levels of GHGs are rising in temperatures (IPCC, 2013b; 2007). This is seen in all CC scenarios and all AOGCMs predict a continent-wide rise in temperature. Africa's antelope species are found across the continent exploiting most of the continent's diverse climate. Some species are subjected to desert conditions where some of Africa's coldest and hottest temperatures are found, while others are also found in the relatively stable tropical forests where the range of temperatures is far smaller. Given that the climate predictions show a general trend of rising temperatures across Africa, it is hypothesized that species adapted for hotter conditions will be better placed to exploit new areas in the future than others (Hypothesis H_1). Therefore species with preferences for hotter temperatures are predicted to perform better and therefore have smaller range contractions or larger expansions, than those with preferences for colder temperatures (Prediction P_1).

Cardillo, *et al*.'s (2008) study of mammalian taxonomic groups, including ungulates, found that species with broad geographic ranges had reduced risk of extinction irrespective of biological differences. Also, chapter three identified that antelope species with existing small ranges are strongly correlated with higher threat status, but neither study considered the impact of CC. There is no standard measure used to assess a species' vulnerability to climate change (Pacifici *et al.*, 2015). Here I use one measure, that of change in range size, to identify species that are vulnerable. Those species with greater contraction in distribution are considered to be more vulnerable. Further, previous studies have identified species existing range size (area of occupancy) as the most important predictor of species extinction risk due to climate change, particularly when linked with certain life history traits such as short generation times (Pearson *et al.*, 2014). The cause of the vulnerability may be due to a greater threat from habitat loss, smaller populations (Cardillo *et al.*, 2008), and/or stochastic events (O'Grady *et al.*, 2004). However, when considering CC and the need for species to disperse into new areas of climatic suitability, there is another consideration related to existing range size. Species with large existing distributions would be expected to have wider climate niches, and are therefore more likely to have connectedness to areas of suitable habitat allowing dispersal in the future, compared with species with a narrow climate niche. Also, given a changing climate, species with a narrow niche are less likely to be able to remain in existing areas as the climate within those areas changes beyond their climatic envelope. With the range of a species correlating strongly with IUCN threat, I hypothesize that species with high threat statuses will be at a greater risk from CC than others as they are less able to

retain existing areas or exploit new areas (H_2). It is therefore predicted that species with increased threatened status will experience a greater contraction in range (Prediction P_2).

The ability to disperse into new areas that become climatically suitable over the coming century may be limited by factors other than connectivity. Unfavourable habitat can prevent species from dispersing. For example, open areas for forest species, roads, and urbanized areas have been identified as barriers to dispersal (Huck *et al.*, 2010; Zimmermann *et al.*, 2005). Antelopes also have the potential to have high habitat fidelity, for example, lechwe species have high fidelity to floodplain areas (Cotterill, 2000). In this study I employ a habitat filter to restrict habitat specialist species (i.e. those species found inhabiting over 90% open or closed habitat type, or specialist grazers, browsers, and frugivores; see 2.7) from entering or dispersing through unfavourable habitat. Given these restrictions, it is hypothesized that specialist species will be less able to exploit areas of climatic suitability in the future due to dispersal limitations (H_3). This would result in specialist species exhibiting greater range contractions or reduced expansion compared with generalist species (P_3).

In this study dispersal velocity of species is based on body mass (Schloss *et al*., 2012) under the optimistic approach, and smaller species therefore have reduced dispersal potential. Consequently, during each time period (i.e. 2030, 2055, and 2080) larger species would be able to expand their range further than small species given equal expansion opportunity. This is essentially an inability to track climate change. This is hypothesized to reduce small species ability to exploit new areas compared to larger species (H_4). It is therefore predicted that there will be a positive relationship between body mass and change in range size (P_4).

Methodology

This study predicts the distribution of Africa's antelopes using SDMs developed in chapter three. For each species, predictions are produced based on integration of the following layers:

1. The climate models (AOGCMs) which are then combined to produce an ensemble forecast.
2. Three climate scenarios (IPCC storylines).
3. Three modelling approaches (referred to as pessimistic, optimistic, and envelope approaches).
4. With and without the habitat filter applied.

Future species distributions modelling

The future predicted distributions were produced using the GLMs developed in chapter three that represent each species' current IUCN distribution (IUCN, 2011). The original models and predictions were developed using the BIOMOD R library (Thuiller, *et al*., 2009) and based on the log of annual precipitation, hottest monthly temperature, and coldest monthly temperature as predictive variables (see chapter three). All climate data was sourced from WorldClim (Hijmans, *et al*., 2005). Current conditions were based on 1950-2000. WorldClim provides monthly average values for minimum and maximum temperature, and precipitation for the 21st century in 10 year periods from 2020-2029 to 2080-2089. The data are at a 10' (arcminute) resolution for all time periods. Future climate groupings were grouped as 2020-2039 (labelled in images as 2030), 2040-2069 (labelled 2055), and 2070-2089 (labelled 2080). Log translation (natural log) was used for precipitation with the mean of the 10 year periods within each climatic period (e.g. 2040-2069) being taken. To find the hottest temperature value, the highest monthly value within each 10 year period for each grid cell was found before the mean across the climatic period was taken; the coldest of the minimum temperatures being taken for the coldest temperature. These were then averaged across the climate groupings.

These climatic period data sets were then used to create the projections using BIOMOD's "projection" command. This takes the forecast data and predicts the probability of the species being in each grid cell based on the new climate data. This uses the model produced in chapter three and the R function "predict" with type set to "response" giving the predicted probabilities.

Climate projections for three different Atmosphere-Ocean Global Circulation Models (AOGCMs) were used to produce the forecasts. They are the United Kingdom Met Office Hadley Centre Coupled Model (UKMO HADCM3), US National Centre for Atmospheric Research Community Climate System Model (NCAR CCSM3), and Norway's University of Bergen, Bjerknes Centre for Climate Research Bergen Climate Model (BCCR BCM2). For each climate model, forecasts were produced for the A1B, A2, and B1 climate scenarios (described below).

A land transformation weighted filter was applied to the forecasted predictions. This reduces the likelihood of species populating areas with a strong human footprint (see Thuiller, *et al*., 2006; Saunderson, *et al*., 2002). Following chapter three, the model for *Oryx dammah* was

poor (see Model performance and refinement) and no projections were made for this species.

Climate scenarios

The IPCC provides a diverse set of climate scenarios offering alternative climatic futures or "storylines". The storylines include various socio-economic environments linked to differing levels of CO_2 production such as fossil fuel intensive (A1FI) to greatly reduced fossil fuel usage (A1T). This study incorporates three climate scenarios, A1B, A2, and B1 (IPCC, 2007).

A1B

The A1 storyline represents a future of great economic growth with a global population that peaks mid-century before declining. It includes the introduction of efficient technologies and a global shift toward regional social equality. The suffix "B" represents a balanced usage of fossil and non-fossil fuel energy sources.

A2

This storyline places continued focus on the individuality of nations and the preservation of local identities rather than globalization. The world population is considered to be continually increasing while technology is slower to develop and remains fragmented at global levels. This scenario represents medium to high greenhouse emissions with continually growing CO_2 emissions (Franklin *et al.*, 2013).

B1

Storyline B1 provides a future based on global solutions to economic, social, and environmental sustainability. This includes the use of green, resource-efficient technologies that reduce material wastage. Greenhouse gas emissions are considered low in this storyline and the world population is the same to the A1 storyline.

Figure 4-1 provides a projection of global surface warming based on each scenario. A2 is considered to produce the highest impact on temperatures, while B1 has the least.

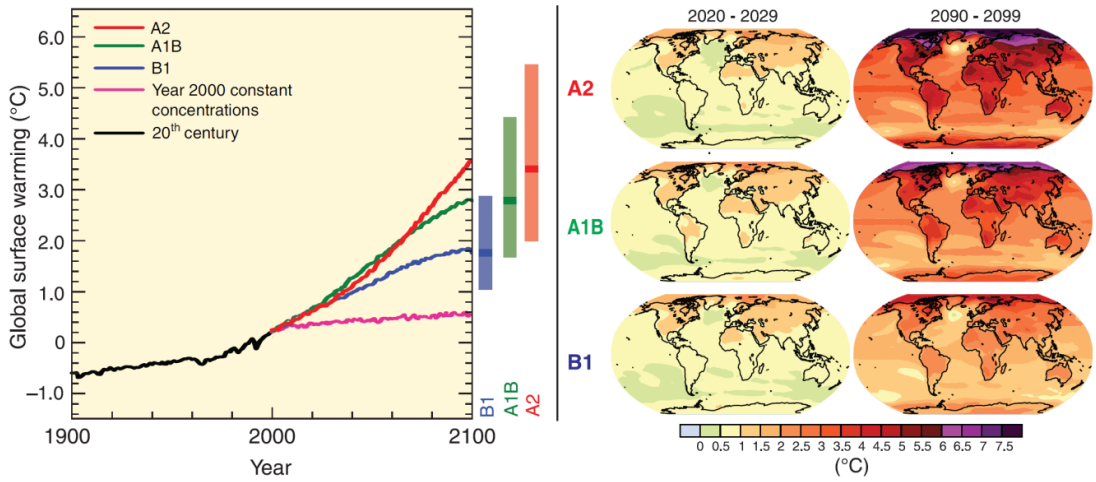

Figure 4-1: Left: Global surface warming based on different climate scenarios and storylines. Right: The global impact of each scenario. Climate scenarios defined by the IPCC (IPCC, 2007). Image altered to include only the scenarios considered herein. Original from IPCC (2007, p.46).

Habitat filter

Each species was categorized as an open or closed habitat specialist, or as a generalist (See 2.7). When producing the forecast distributions specialist species were unable to enter unfavourable habitat and all species were unable to enter urbanized areas. This is demonstrated in Figure 4-2 and Figure 4-3. In Figure 4-2 the Aders' duiker, a closed habitat specialist, is restricted in its dispersal by habitat whereas in Figure 4-3 it is not. In this direct comparison Aders' duiker's future suitable range is highly restricted due to open habitat and human dominated areas (Figure 4-2:middle) leading to no suitable areas in the 2055 period. When unrestricted (Figure 4-3) the species range expands widely in the 2030 period (Figure 4-3:top right), shifts range to the southwest in the 2055 period (Figure 4-3:bottom left) before being lost completely in the final forecast period (Figure 4-3:bottom right).

Pessimistic, optimistic, and envelope modelling approaches

Three modelling approaches were used to assess the impact of climate change on the distribution of species. In all approaches species may be limited by habitat filter when in use. The first two approaches provide an optimistic and pessimistic view of species distributions in the future. The pessimistic model assumes that expansion of range cannot occur based on the assumption that human pressures are prohibitive. Therefore, the future range of each species can remain stable or contract as climatic conditions change over time.

In contrast to the pessimistic approach, the optimistic approach allows expansion of a species' range, outside of its current range. Each species has a yearly dispersal velocity assigned, based on Schloss, *et al*. (2012), and may disperse depending on connectivity where

future range must be connected to existing range over time (see 2.8). Figure 4-4 demonstrates the potential for a species' range to be restricted by dispersal ability. These species' ranges can expand or contract. This approach suggests that there is a relaxation of human pressures in that species will not only be allowed to disperse into new suitable areas, but also currently suitable areas from which the species happen to be absent at present.

Finally, the envelope approach considers a species' distribution to be the area of suitable conditions based on the original model. The starting point is the models prediction of suitable conditions that are currently connected (see 2.8) to the IUCN distribution. Expansion or contraction of this range can then occur. Expansion of range is not limited by dispersal, but must have connectivity to future areas and may be limited by the habitat filter if applied. The envelope approach is suggestive of what the species' distribution would be without human intervention, dispersal limitations, and any possible niche displacement.

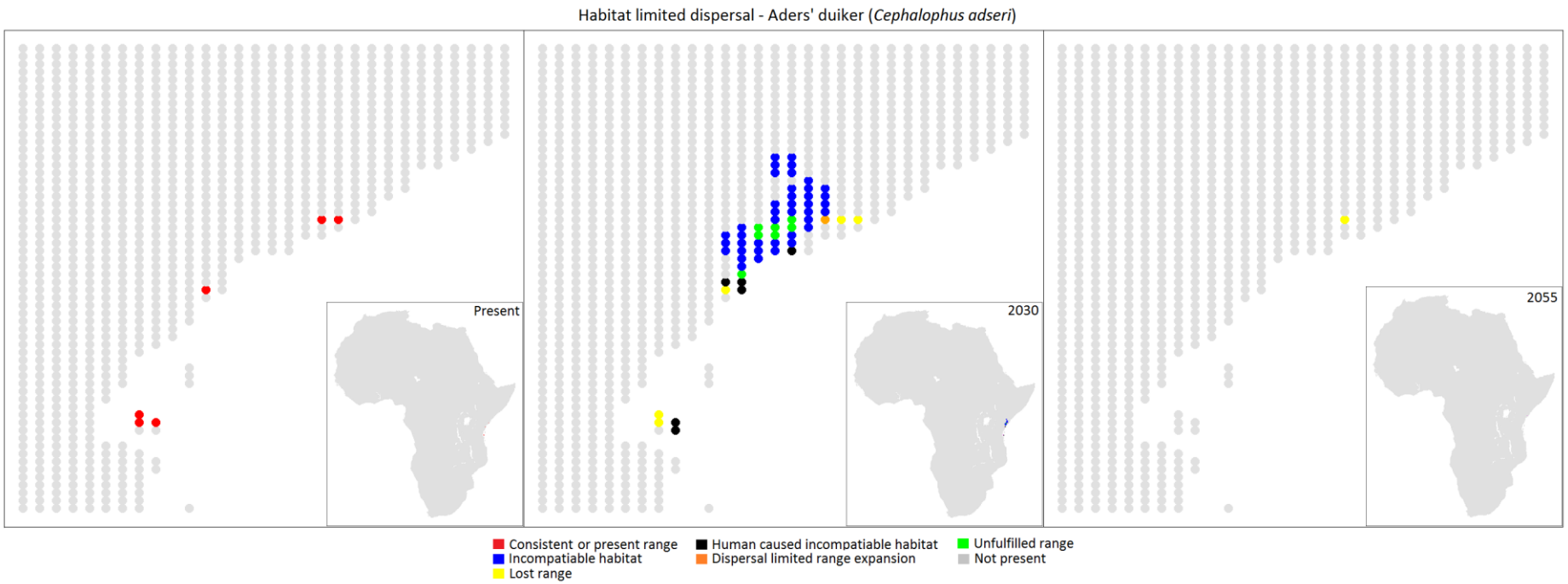

*Figure 4-2: For comparison with Figure 4-3 - The impact of habitat type on the forest dwelling Aders' duiker (*Cephalophus adersi*). Left: The current IUCN range including the island of Zanzibar (red). Middle: The predicted distribution in 2030. Some areas are no longer suitable climatically (yellow – West Zanzibar and Kenya), human dominated areas are unavailable (black – East Zanzibar including a new area that would have become potentially viable), incompatible open habitat (blue – Kenya), range expansion limited by dispersal pace (orange – one grid cell in Kenya), and areas which are climatically suitable but not realized is due to habitat barriers as dispersal is not possible. Right: Loss of the remaining climatically suitable area in 2055 (pink). Predictions are based on the A1B climate scenario from the United Kingdom Met Office Hadley Centre Coupled Model.*

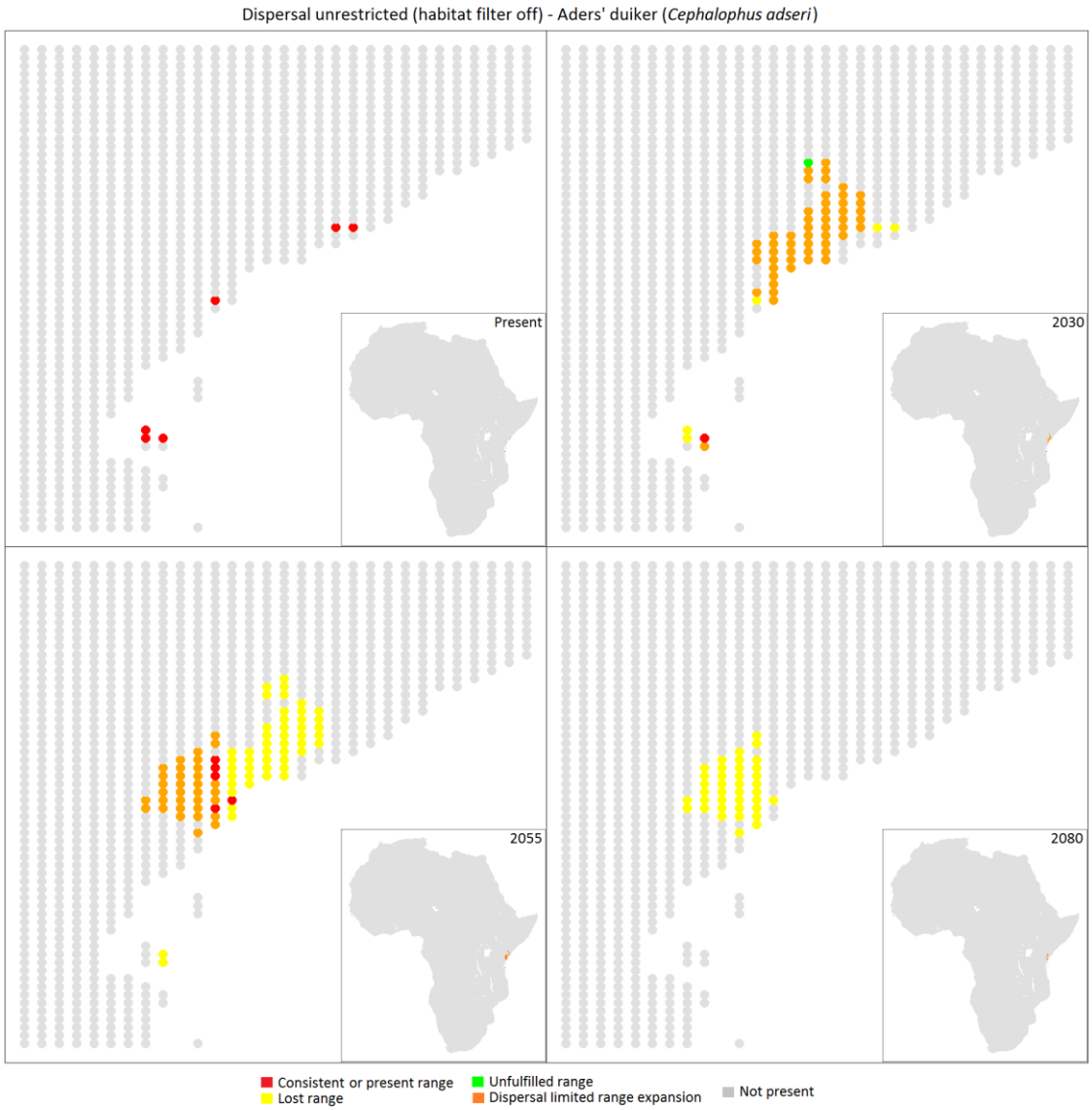

*Figure 4-3: For comparison with Figure 4-2 - The suitable areas for Aders' duiker (*Cephalophus adersi*) if dispersal is unrestricted by habitat suitability. Clear differences are seen in 2025 (top right) as the species expands (orange) into suitable areas but is restricted by dispersal pace (green), expansion seen in southern Zanzibar and losses (yellow) in the west of the island. Mainland suitable areas then expand to the west, but are lost in the east (2055 – bottom left) before all areas are lost by 2085 (bottom right). Predictions are based on the A1B climate scenario from the United Kingdom Met Office Hadley Centre Coupled Model.*

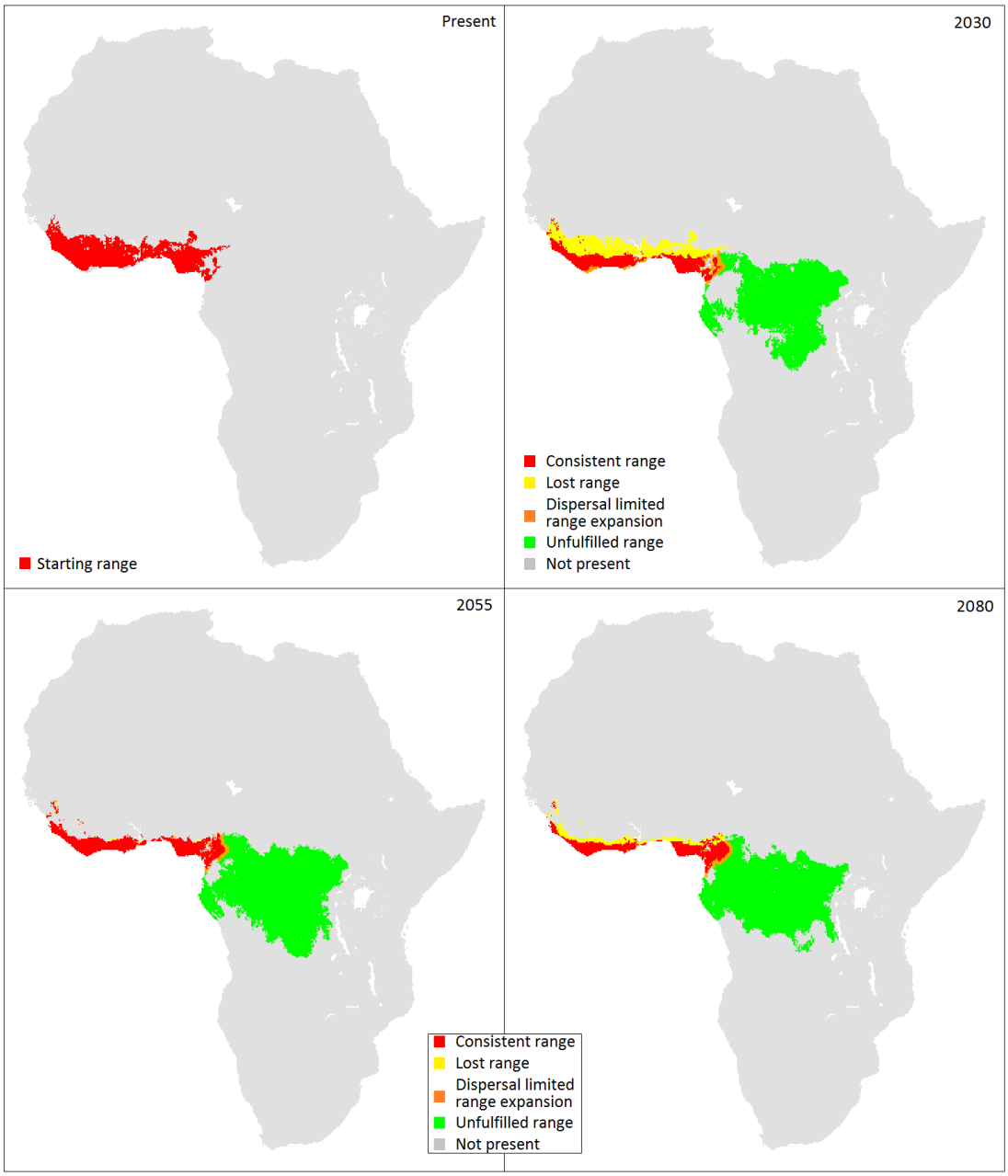

*Figure 4-4: Example of future range being limited by the dispersal ability of royal antelope (*Neotragus pygmaeus*). Top left is the present day distribution based on the ensemble envelope model methodology, i.e. not the IUCN distribution. Top right is the 2030 projection. Consistent range is the predicted range present both in the previous time period and 2030. Lost range is range present in the previous time period and not in 2030. Dispersal limited range expansion is areas not present in the previous time period but predicted for 2030* ***and*** *reachable in that time period based on dispersal pace. Unfulfilled range is areas predicted for 2030, but not reachable in the time period. Bottom left is the projection to the 2055 time period with the bottom right following that as the 2080 time period. Predictions are based on the A1B climate scenario from the United Kingdom Met Office Hadley Centre Coupled Model.*

Ensemble forecasts

In the past, species distribution modelling and forecasting studies have typically utilized a single AOGCM's prediction of future climate, possibly with various climate scenarios, to predict future species distributions. The African continent's climate is difficult to predict

(Boko *et al.*, 2007) resulting in climate models from different organizations displaying inconsistencies. Here, to provide greater confidence in the results, multi-climate-model ensemble forecasts (hereafter 'ensemble forecasts') were produced for each species that combine species distribution predictions based on three AOGCMs climate predictions. These are different to ensemble projections created using multiple model methodologies (e.g. GLM, GAM, RF, CTA, MAXENT, etc.; see Araújo & New, 2007) that typically use a single AOGCM's climate predictions.

To create an ensemble forecast, a prediction of suitable conditions is produced for each species using climate projections from the three AOGCMs. These are overlain to produce an integer value between 0-3 (0 = no model predicts presence, to 3 = all models predict presence). Figure 4-5 shows an example of the ensemble forecast. Areas where multiple predictions agree provide a greater confidence that suitable conditions will be found in those areas. In this thesis, the results are based on species distributions where two or three of the model predictions overlap.

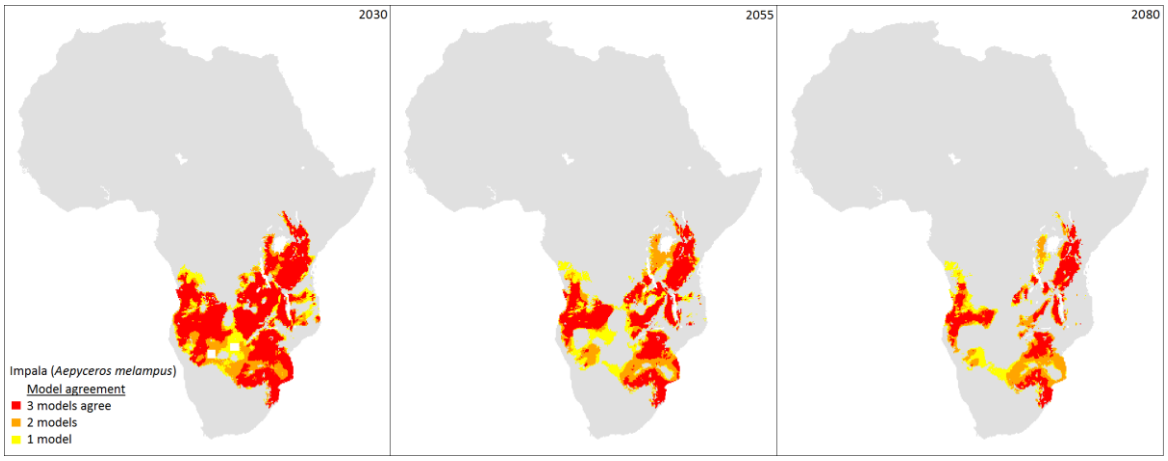

*Figure 4-5: Ensemble forecast for the impala (*Aepyceros melampus*) in 2030, 2055, and 2080 using climate scenario A1B (envelope projection). Red indicates that all three climate models agree that the species will be present, orange shows two of the three models agreeing, and yellow where only one model predicting suitable areas.*

Niche breadth

To assess the niche breadth and position of species, and the correlation of niche properties to range change size, I used the outlying mean index (OMI) analysis (Thuiller *et al.*, 2012) implemented in the *ade4* R library (Chessel *et al.*, 2004). The advantages of OMI is that it makes no assumptions regarding the shape of a species response curve to the environment, and it gives equal weight to species-rich and species-poor areas (Baastrup-Spohr *et al.,* 2015; Thuiller *et al.,* 2012). The OMI uses principal components analysis (PCA) to produce a set of

ordination axes, and the loadings for each climate variable on those axes. These indicate the degree that combinations of climate variables affect the distribution of species in different areas (Baastrup-Spohr *et al.,* 2015). The OMI methodology uses each species' existing IUCN distribution, and the climatic conditions therein, to find the niche breadth and position within the environmental space. Niche breadth is the variability (s.d.) of the environment used by each species along the axes. Niche position is the distance between the mean conditions of the species and the mean conditions of the study area. OMI also provides a measure to assess whether species select marginal environments over common environments (Thuiller *et al.,* 2012). A high OMI value indicates a species' environmental conditions differ from the average conditions and show a high degree of specialization (Baastrup-Spohr *et al.*, 2015). The data for the variables used in calculating the OMI values were taken from the same sources as used to produce the model (see 2.5.3).

Modelling summary

A summary of the modelling methodology is as follows (also see Figure 4-6):

1. The 73 species distributions are modelled for the current time period (1950-2000 climate).
2. Projections of distributions are produced for the three climate models and three climate scenarios.
3. The land transformation filter is applied to create an additional set of predictions.
4. Connectivity of areas is calculated for each projection with and without the habitat filter.
5. The three projection types are produced, i.e. envelope, optimistic, pessimistic. Dispersal throughout the connected areas is modelled for the optimistic and pessimistic approaches; for the pessimistic approach, dispersal is only allowed within the species' existing range (i.e. where an area becomes unsuitable, then at a later stage becomes suitable again).
6. The predictions for the three climate models are collated to produce the ensemble forecasts.

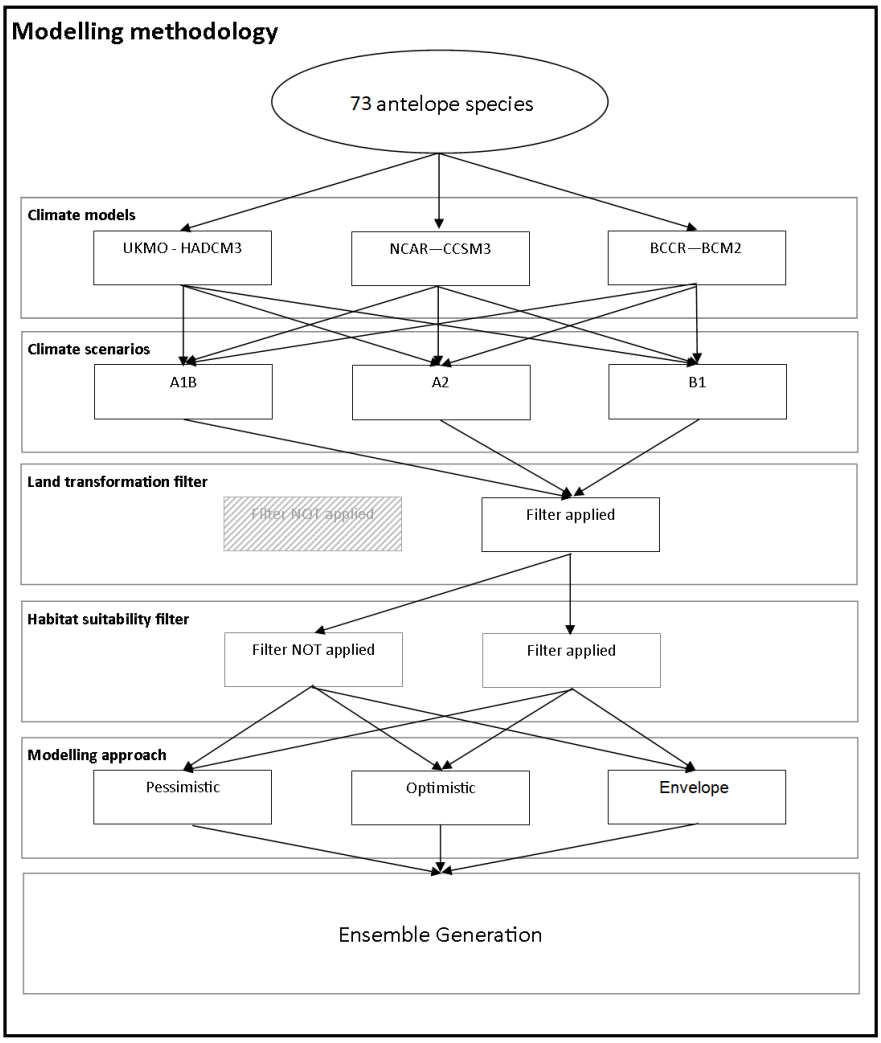

Figure 4-6: Overview of modelling methodology. 73 species modelled against 3x climate models, each with 3x climate scenarios. The land transformation filter is always applied. Habitat suitability is both applied and not. Three projection types are then created before the collation of the climate models into ensemble models.

Post-prediction modelling

The contraction or expansion of suitable range for each species was calculated for each of the three approaches, for each of the climate scenarios, and for when the habitat filter was applied and not applied. GLM models were produced to identify the variables that predict range contraction/expansion. The variables included in the models were: species optimal conditions (log of annual precipitation, hottest and coldest temperatures), temperature range (hottest minus coldest optimal temperature), log of mass, shoulder height, percentage of different forage types in the diet (fruit, browse and grass), horn length, group size, IUCN threat status, habitat specificity (generalist/specialist [i.e. open or closed], generalist/open/closed), diet diversity, and log of global range. The optimal conditions for

hottest and coldest temperatures, as well as for annual precipitation were derived from the original models that predict the species' distribution. This was achieved using the quadratic component of the model to find the vertex value indicating the optimal value. If the values produced were outside of the range found in Africa then the minimum or maximum values for the continent were used. If the variable was not present for a species' model, and therefore no value was available (i.e. it had been dropped during the model generation by the stepwise regression), then the mean value for that species' range was used.

The best performing model was found using the "stepAIC" function from the R library MASS (Ripley, 2014) starting from a complete model, including all variables, and where the stepwise search mode was set to both directions. Covariance between variables was assessed using the "rcorr" function from the R library Hmisc and were used to calculate Pearson linear correlations (Harrell Jr., 2014) to reduce the possible impact of multicollinearity. IUCN and global range were not included in the same models because they are strongly negatively correlated (Pearson's r= -0.7; p<0.001). In addition, adult mass, horn length, shoulder height, and dispersal pace were strongly correlated and were not paired in any models. R^2 values were used to determine strength of correlation values (r) and grouped as per Fowler *et al.* (1998).

Models including IUCN threat status as a variable excluded the silver dik-dik (*Madoqua piacentinii*) as it has no IUCN threat category being listed as data deficient (n=72). Where dietary variables were used, two species were excluded as no data was available (Mongalla gazelle [*Eudorcas albonotata*], and Cuvier's gazelle [*Gazella cuvieri*]), resulting in a sample size of 71.

Analysis of variance (ANOVA) was used to compare the results from different climate models, both with and without the application of the habitat filter. Tukey and Bonferroni post hoc tests were conducted to identify significant variables/models (smallest interval selected).

Phylogenetic signal

The R package 'geiger' fitContinuous function was used to evaluate whether any phylogenetic signal was present in the models of species range changes (English *et al.*, 2012; Walls, 2011). No phylogenetic signal was found for any of the datasets and therefore no models are presented with phylogenetic control.

Results

The combination of modelling approaches, climate scenarios, and the habitat filter result in a highly detailed set of results. Here I focus on the changes that are predicted to take place between the present and the 2080 climatic period. In addition, I focus on the A1B climate scenario with references to the higher and lower emission scenarios (A2 and B1 respectively based on Figure 4-1). Each of the modelling approaches are presented with and without the habitat filter applied. These results are summarized in Table 4-2. Table 4-3 and Table 4-4 present the species that are predicted to perform worst and best respectively, i.e. those having the largest contraction (worst) and largest expansion/smallest contraction (best) in range. ANOVA results identifying differences between the habitat filter application and the three climate models used to produce the ensemble model are in Table 4-5. The variables that predict the change in range size are presented for each modelling approach, by climate scenario, and by habitat filter application (Table 4-6 - Table 4-8).

Species range changes - contraction or expansion?

Table 4-2 summarizes the change in range from present to 2080 based on the ensemble forecasts and broken down by model approach, climate scenario, and habitat filter application. The average range remaining (ARR) values are the average percentage change for all species from present to the 2080 period. The average contraction (AC) is a subset of the species which exhibit a shrinking of range. The value is the average percentage contraction between present and 2080. Finally, average expansion (AE) is the percentage increase for those species exhibiting an expansion. Therefore an average of 21% increase represents an ARR of 121%. Under the envelope and optimistic approach a species' range may shift, expand, or contract. Under the pessimistic approach the species' ranges can only remain constant or contract.

In each model approach across all options, the hirola is found to have no suitable connected range by 2080. Five other species (addax, Aders' duiker, dibatag [*Ammodorcas clarkei*], Nile lechwe [*Kobus megaceros*], and dama gazelle), also have no suitable range depending on modelling approach, climate scenario, and habitat filter application (Table 4-2).

Envelope approach

The envelope approach evaluates the predicted range of species based on suitable climatic conditions that are connected to the existing distribution and unlimited by dispersal. Note that present conditions are therefore represented by suitable climatic conditions rather than

actual distribution. Under the A1B climate scenario, and without the habitat filter applied, range contraction is predicted for 59 of the 73 species (80%), with an average range remaining (ARR) of 70%. The B1 climate scenario has predictions of range contraction for 62 species (85%) with an ARR of 68%. The A2 climate scenario has a 63% ARR. The A1B climate scenario's average expansion (AE) is 21% and average contraction (AC) is 42%. Nineteen species are predicted to have a range contraction of over 50% under the A1B scenario rising to 21 for the B1 scenario, and 32 under the A2 scenario (16, 18, and 29 respectively with the habitat filter applied).

The differences found when applying the habitat filter were only statistically significant for some species (Table 4-5a top row). In addition to the hirola, the Aders' duiker exhibits a 100% contraction of range when the filter is applied due to dispersal limitation through incompatible habitat and human dominated areas. The application of the habitat filter does not affect the number of species that are predicted to contract or expand their range. However, with the habitat filter applied AC is slightly lower (40%), while AE and ARR are slightly higher (22% and 72% respectively). This may seem contrary to logic where the habitat filter should restrict range. The reason for this is that the starting distribution, which is based on climatic suitability for the envelope approach, is also restricted by the habitat filter. Therefore some areas that are currently climatically suitable will be removed by the habitat filter; this reduces the range size for the starting distribution of those species. Over the century this affects the proportional contraction/expansion in range.

Pessimistic approach

All species by necessity exhibit either no change or a contraction in range under the pessimistic approach where they are unable to disperse. Under the A1B climate scenario, without the habitat filter applied, ARR is 64% with 16 species exhibiting a contraction of range greater than 50%; with the habitat filter applied ARR was 63% and 18 species experienced a contraction greater than 50%. No species retained 100% of its range, the highest being the dorcas gazelle with 99.95% retained (99.98% habitat filter applied). AC is 36% (range 35% to 42% under the B1 and A2 climate scenario respectively) and statistically similar with the habitat filter applied (Table 4-5a top row). Four species (addax, Aders' duiker, hirola, and Nile lechwe) have a complete loss of range rising to six (dibatag and dama gazelle) under the A2 climate scenario. Only the hirola has a complete loss of range under the B1 climate scenario, although Aders' duiker also has complete loss of range with the habitat filter applied. All six species are already threatened (Table 4-1). The silver dik-dik

retains only 1% of its range; this species does not currently have a threatened status due to data deficiency.

Species	Scientific name	Range remaining (%)	Current IUCN threat status
Addax	*Addax nasomaculatus*	*0*	Critically Endangered
Aders' duiker	*Cephalophus adersi*	*0*	Critically Endangered
Dama gazelle	*Nanger dama*	*0*	Critically Endangered
Hirola	*Beatragus hunteri*	*0*	Critically Endangered
Nile lechwe	*Kobus megaceros*	*0*	Endangered
Dibatag	*Ammodorcas clarkei*	*0*	Vulnerable
Silver dik-dik	*Madoqua piacentinii*	*1*	Data Deficient

Table 4-1: Species predicted to have 0-1% of their existing range remaining by climate period 2080 based on the pessimistic modelling approach and climate scenario A2 irrespective of habitat filter application. Ordered by IUCN threat status.

Figure 4-7 demonstrates the current IUCN distribution of the seven species listed in Table 4-1 that have 99-100% range contraction under the A2 climate scenario using the pessimistic modelling approach.

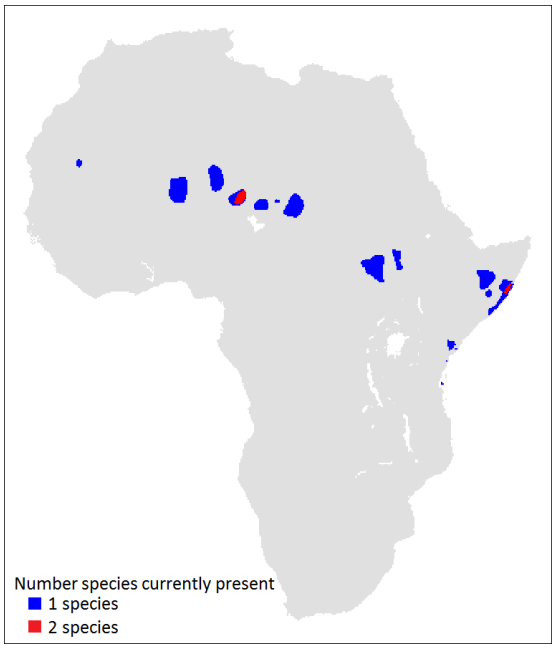

Figure 4-7: Current IUCN distribution of species predicted to have 99-100% range contraction (A2 scenario) including overlapping species numbers.

Optimistic approach

The optimistic approach allows species to disperse from their existing range. For all climate scenarios the ARR is greater than 100% and more species demonstrate range expansion than contraction (Table 4-2). Under the A1B climate scenario 29 species have a predicted range contraction with an AC of 40%, (maximum 34 species and AC of 44% under the A2 climate

scenario). Seven species are predicted to have a range contraction over 50% (maximum 9 under the A2 climate scenario). The A1B climate scenario has two species (hirola and Nile lechwe) predicted to be without suitable areas when the habitat filter is not applied, whereas scenarios A2 and B1 have only one (hirola). This also applies when the habitat filter is on except that B1 has two species without any suitable range (hirola and Aders' duiker). Under the A2 climate scenario two additional species have only a single grid cell of suitable conditions remaining (Nile lechwe and silver dik-dik).

Under the A1B climate scenario AE is predicted at 96.51, almost doubling the range of 44 species (113.21% with the habitat filter applied). The AE values are higher when the filter is applied for A2 and A1B, but reduced for the B1 climate scenario. However, there is no statistical difference between ARR values with and without the habitat filter application (Table 4-5a top row).

Successful species

The results above focus on the species not performing well under climate change. However, some species are predicted to have range expansion under the optimistic and envelope approaches. Table 4-4 presents those species with the top five range expansions for each modelling approach (except that least range contraction is shown for the pessimistic approach) split both by habitat filter application and combined. In contrast Table 4-3 presents the worst performing species, i.e. those species with the greatest contraction in range across the three approaches.

There were no obvious relationships between the species in Table 4-3 and Table 4-4 with regard to morphology, ecology, or optimal climatic conditions. Table 4-4 shows that the species that consistently perform well are largely split into two groups; a: those that perform well under the envelope and pessimistic approach; b: those that perform well under the optimistic approach. The only species not adhering is the nyala (*Tragelaphus angasii*).

			Species range (all)		Species range (contraction only)								Species range (expansion only)		
	Model approach	Climate scenario	Average range remaining	Standard deviation	Total	Average contraction	Standard deviation	>50%	>75%	>90%	100%	Species with 100% contraction	Total	Average expansion	Standard deviation
Habitat Filter Off (73 Species)	Envelope	A2	63.40%	0.374	59	50.11%	0.163	32	11	5	1	Bh	14	20.31%	0.164
		A1B	70.05%	0.354	59	42.13%	0.174	19	9	4	1	Bh	14	21.38%	0.174
		B1	68.18%	0.326	62	40.89%	0.258	21	8	3	1	Bh	11	19.31%	0.136
	Pessimistic	A2	57.52%	0.303	73	42.48%	0.303	29	12	7	6	An,Ac,Bh,Ca,Km,Nd			
		A1B	64.09%	0.291	73	35.91%	0.291	16	10	6	4	An,Bh,Ca,Km			
		B1	64.62%	0.279	73	35.38%	0.279	21	9	5	1	Bh			
	Optimistic	A2	122.80%	1.151	34	44.36%	0.271	9	7	3	1	Bh	39	81.35%	1.301
		A1B	142.45%	1.377	29	39.58%	0.275	7	6	2	2	Bh, Km	44	96.51%	1.540
		B1	138.46%	1.333	33	35.70%	0.296	8	4	3	1	Bh	40	99.65%	1.536
Habitat Filter On (73 Species)	Envelope	A2	64.68%	0.369	59	49.01%	0.163	29	12	6	2	Bh, Ca	14	17.57%	0.158
		A1B	71.95%	0.358	59	39.92%	0.279	16	9	5	2	Bh, Ca	14	21.97%	0.167
		B1	70.34%	0.334	62	39.39%	0.270	18	8	4	2	Bh, Ca	11	19.81%	0.115
	Pessimistic	A2	56.25%	0.303	73	43.75%	0.303	29	12	8	6	An,Ac,Bh,Ca,Km,Nd			
		A1B	63.00%	0.292	73	37.00%	0.292	18	10	6	4	An,Bh,Ca,Km			
		B1	63.40%	0.288	73	36.60%	0.288	22	10	6	2	Bh, Ca			
	Optimistic	A2	125.14%	1.623	34	41.20%	0.277	10	7	3	1	Bh	39	110.15%	2.165
		A1B	140.03%	1.767	29	35.19%	0.280	7	6	2	2	Bh, Km	44	113.21%	2.248
		B1	116.44%	1.029	33	37.61%	0.299	10	5	4	2	Bh, Ca	40	71.99%	1.209

Table 4-2: Detailing the change in predicted contraction/expansion range in the future sub-divided by model approach, climate scenario, and whether the habitat filter is applied. The table provides average range remaining (ARR) for all species, and then contracting (AC) and expanding (AE) species separately. Along with the total number of species with expansion and contraction are the number of species exhibiting contractions over 50, 75, and 90%, and those showing 100% contraction (no suitable range remaining). The pessimistic model approach does not allow for expansion. Note ARR, AC, and AE are calculated differently. Where $\boldsymbol{ARR = (2080\ range/current\ range) * 100}$, $\boldsymbol{AC = (|(2080\ range/current\ range) - 1|) * 100}$, *and* $\boldsymbol{AE = ((2080\ range/current\ range) - 1) * 100}$. *ARR and AE are calculated using the same methods. Species codes refer to* Addax nasomaculatus *(An),* Ammodorcas clarkei *(Ac),* Beatragus hunteri *(Bh),* Cephalophus adersi *(Ca),* Kobus megaceros *(Km), and* Nanger dama *(Nd).*

	Habitat filter not applied				Habitat filter applied				Combined (habitat filter on and off)			
Species	Envelope	Pessimistic	Optimistic	Across all	Envelope	Pessimistic	Optimistic	Across all	Envelope	Pessimistic	Optimistic	Across all
Beatragus hunteri	3	3	3	9	3	3	3	9	6	6	6	18
Kobus megaceros	3	3	3	9	3	3	3	9	6	6	6	18
Madoqua piacentinii	3	3	3	9	3	2	3	8	6	5	6	17
Cephalophus leucogaster	3	0	3	6	3	1	3	7	6	1	6	13
Cephalophus adersi	2	3	0	5	3	3	1	7	5	6	1	12
Neotragus batesi	3	0	3	6	3	0	3	6	6	0	6	12
Cephalophus callipygus	3	0	3	6	3	0	2	5	6	0	5	11
Addax nasomaculatus	0	3	2	5	0	3	2	5	0	6	4	10
Nanger dama	1	3	1	5	0	3	1	4	1	6	2	9
Ammodorcas clarkei	0	3	0	3	0	3	0	3	0	6	0	6

Table 4-3: List of species predicted to have the largest contraction in range. Those species predicted to have the seven largest contractions of suitable conditions are grouped by modelling approach including all scenarios (i.e. envelope combines the predictions for the A1B, A2, and B1 climate scenarios). Therefore a value of "3" indicates that a species had one of the seven largest contractions of range under all climate scenarios) and then grouped by habitat filter and finally combined.

	Habitat filter not applied				Habitat filter applied				Combined (habitat filter on and off)			
Species	Envelope	Pessimistic	Optimistic	Across all	Envelope	Pessimistic	Optimistic	Across all	Envelope	Pessimistic	Optimistic	Across all
Cephalophus ogilbyi	2	2	3	7	2	1	3	6	4	3	6	13
Kobus kob	3	3	0	6	3	3	0	6	6	6	0	12
Redunca redunca	3	1	0	4	2	1	0	3	5	2	0	7
Tragelaphus angasii	1	0	3	4	1	0	2	3	2	0	5	7
Tragelaphus eurycerus	1	2	0	3	2	2	0	4	3	4	0	7
Dorcatragus megalotis	0	0	3	3	0	0	3	3	0	0	6	6
Gazella dorcas	0	3	0	3	0	3	0	3	0	6	0	6
Kobus leche	0	0	3	3	0	0	3	3	0	0	6	6
Ourebia ourebi	0	3	0	3	0	3	0	3	0	6	0	6
Philantomba maxwellii	3	0	0	3	3	0	0	3	6	0	0	6
Nanger soemmerringii	0	0	1	1	0	0	3	3	0	0	4	4
Hippotragus equinus	1	1	0	2	0	1	0	1	1	2	0	3
Cephalophus adersi	0	0	2	2	0	0	0	0	0	0	2	2
Cephalophus rufilatus	1	0	0	1	1	0	0	1	2	0	0	2
Cephalophus dorsalis	0	0	0	0	0	1	0	1	0	1	0	1
Gazella cuvieri	0	0	0	0	0	0	1	1	0	0	1	1
Raphicerus melanotis	0	0	0	0	1	0	0	1	1	0	0	1

Table 4-4: List of species predicted to have the largest expansion (envelope and optimistic approaches) or smallest contraction (pessimistic approach) of range. Those species predicted to have the five largest expansion of suitable conditions are grouped by modelling approach including all scenarios (i.e. envelope combines the predictions for the A1B, A2, and B1 climate scenarios). Therefore a value of "3" indicates that a species had one of the five largest expansions/smallest contraction of range under all climate scenarios) and then grouped by habitat filter and finally combined.

Comparison of climate models, scenarios, and habitat filter application

Table 4-5a highlights that there is no effect when applying the habitat filter to the ensemble forecasts across all approaches and climate scenarios. Differences are found between the three climate models used to produce the ensemble model (Table 4-5a). This is important when considering whether one or more of the models could be influencing the ensemble production adversely. There are a number of significant differences between the models. The same relationships are found with or without the habitat filter.

Which model or models are producing these significant results provide insight into whether one model is driving the ensemble model production. For that reason Bonferroni *post hoc* tests were conducted. In the envelope approach scenario B1, the CCSM3 model was significantly different to HADCM3 ($p=0.001$) and BCM2 ($p<0.001$). This result was the same for the habitat filter application.

For the pessimistic results each climate scenario showed significant differences. Both scenario A2 and A1B showed similar differences whereby HADCM3 was significantly different to both CCSM3 (A2 $p=0.045$; A1B $p=0.042$) and BCM2 (A2 $p=0.004$; A1B $p=0.048$). For the pessimistic approach scenario B1 significant differences were found between all climate models (HADCM3:CCSM3 $p<0.001$; HADCM3:BCM2 $p=0.016$; CCM3:BCM2 $p<0.001$). The habitat filter application has the same relationships for all scenarios with marginally altered p-values (± 0.01) with all remaining significant.

In the optimistic approach the A2 scenario demonstrated a difference only between HADCM3 and BCM2 ($p=0.012$) with a similar result when the habitat filter is applied ($p=0.018$). The A1B scenario has no significant differences between the climate models without the habitat filter applied, but is significant with it applied ($p=0.049$). However, further analysis shows no significance between the individual climate models (min p-value=0.074 [HADCM3:BCM2]). Finally, the B1 scenario (habitat filter applied) has differences between CCSM3 and BCM2 ($p<0.001$). When the habitat filter is applied this difference remains and an additional difference is found between HADCM3 and BCM2 ($p=0.007$). More differences between climate models are seen between HADCM3 and BCM2 ($n=9$) while both other relationships (HADCM3:CCSM3 and CCSM3:BCM2) had four differences.

Table 4-5b demonstrates that there is no significant difference in the ensemble results across the climate scenarios irrespective of habitat filter application or modelling approach.

a		Model approach	Climate scenario	p=	sig	Model approach	Climate scenario	p=	sig	Model approach	Climate scenario	p=	sig
	Ensemble comparison (habitat filter on/off)	Envelope	A2	0.836		Pessimistic	A2	0.801		Optimistic	A2	0.920	
			A1B	0.747			A1B	0.821			A1B	0.927	
			B1	0.694			B1	0.796			B1	0.266	
	Comparison between climate models (habitat filter off)	Envelope	A2	0.148		Pessimistic	A2	0.004	**	Optimistic	A2	0.013	*
			A1B	0.2956			A1B	0.023	*		A1B	0.090	.
			B1	8.42E-06	***		B1	2.20E-16	***		B1	6.86E-05	***
	Comparison between climate models (habitat filter on)	Envelope	A2	0.137		Pessimistic	A2	0.004	**	Optimistic	A2	0.018	*
			A1B	0.252			A1B	0.020	*		A1B	0.049	*
			B1	4.05E-06	***		B1	2.20E-16	***		B1	1.78E-05	***

b		Model approach	Habitat filter	p=	sig	Model approach	Habitat filter	p=	sig	Model approach	Habitat filter	p=	sig
	Ensemble comparison across climate scenarios	Envelope	Off	0.501		Pessimistic	Off	0.262		Optimistic	Off	0.624	
			On	0.428			On	0.259			On	0.634	

*Table 4-5: ANOVA comparisons of model results split into categories. Table "**a**" compares the variance in the range contraction/expansion based on the ensemble forecast and also compares based on the habitat filter being on/off (top row). This is sub-divided by modelling approach (envelope/pessimistic/optimistic) and climate scenarios. The following two rows compare the range contraction/expansion variance in each climate model (HADCM3, CCSM3, and BCM2) sub-divided as before. Table "**b**" compares the variance in range contraction/expansion between climate scenarios (A2, A1B, B1) for each modelling approach and with/without the habitat filter on.*

Variables predicting future range change

Based on the data summarized above, further analysis was conducted to establish the species variables that predict change in range size. Two sets of analyses were run including either IUCN threat or global range due to the high correlation between these variables. The results with the more significant p values and higher R^2 values were taken as the final model. The models were produced using the stepAIC R function. The analysis moreover included all species trait variables as described in the methodology. Only IUCN threat, global range, and the climatic variables were retained in the models. The final models show that all ecological, behavioural, and morphological variables were removed through the stepwise regression. Models were also produced without IUCN, global range, and climatic variables to identify species trait variables that may have been masked by the strength of other variables. Following the same stepAIC methods the models produced were all found not significant (results not shown). In the following, the results are presented according to modelling approach.

Envelope approach

Optimal hottest temperature and IUCN threat status were consistently important in predicting range change using the envelope approach (Table 4-6). These two variables were thus included in all six models, i.e. irrespective of climate scenario or habitat filter application. Optimal hottest temperature was positively correlated, while IUCN threat was negatively correlated with range change, i.e. the more threatened species having a greater reduction in range and those species with hotter preferences performing better. The A1B and A2 scenario without the habitat filter (first and third row), also included a positive relationship with optimal coldest temperature (i.e. species preferring warmer coldest conditions have greater increases/smaller contractions in range). The p-values for the models are all highly significant. The R^2 values ranged from 0.354 to 0.436 indicating moderately strong relationships.

Models where IUCN threat status was replaced with global range, a highly correlated variable, produced similar relationships, but these models had lower p and R^2 values.

Pessimistic approach

IUCN threat status is highly significant as a predictive variable in predicting range change under the pessimistic approach ($p<0.001$ in all models; Table 4-7). This supports the

envelope approach results in that IUCN category is a valuable predictor of range change. As with the envelope approach, the models also include optimal hottest temperature, although this variable was not statistically significant (p>0.05) in the B1 models. The models' p-values are all significant (p≤0.001 for all models). The R^2 values (range 0.174 – 0.216) indicate modest strength relationships.

Optimistic approach

The optimistic approach presents differing results from the envelope and pessimistic approaches (Table 4-8). Only three models were produced using the stepAIC function (other models: p=1; R^2=0) and included global range instead of IUCN threat; these models were all produced for results without the habitat filter applied. The global range correlation with predicted range change was negative indicating that species with a smaller original distribution will experience a greater proportional expansion in range. The models predicting range change under the A1B and B1 climate scenario were both significant (p=0.037 and 0.019 respectively). The A1B model had a low R^2 value (0.059). The B1 model, which included optimal hottest temperature as a non-significant predictive variable, had an R^2=0.105 indicating a moderately weak correlation. The model based on the predictions from the A2 climate scenario was not significant (p=0.634).

Dispersal ability under the optimistic approach

In general, dispersal ability was not found to be a limiting factor for antelopes. Analysis of the unfulfilled grid cells, i.e. those cells that were connected to a species range but the species' dispersal pace did not allow them to reach those areas within the time period, shows that the percentage of species with no remaining unfulfilled grid cells in the final time period was 76% with and without the habitat filter applied. Therefore, most species were predicted to be able to keep up with climatic change. The average percentage of range that was unfulfilled was <1% (mean=0.61%; s.d.=0.040 without filter; mean=0.39%; s.d.=0.022 with filter). There were no significant correlations between any of the species morphological traits and species able to keep up with climate change, and those that could not (all models p>0.1).

Change in climatic predictor variables

There is a greater predicted change in the temperature variables than precipitation between present day and 2080 conditions (see Table 4-9). ANOVA of the changes yielded significant difference between climate variables ($F_{(2,6)}$=8.022; p=0.02), but not between the climate scenarios (p=0.18) when added to the analysis. Tukey HSD comparisons indicated significant

differences between precipitation and both hottest and coldest temperature ($p<0.05$), but not between hottest and coldest temperature variables themselves ($p>0.05$). There is also a trend towards a difference in variation between the change in climatic conditions ($p=0.06$), which Tukey HSD comparisons indicates is between the coldest temperature and precipitation ($p=0.054$).

The greater level of variation in precipitation is partially related to the uncertainty in the Sahel region (Hulme *et al.*, 2001) resulting in differences in the projected precipitation patterns for each of the AOGCMs. To identify if species in this area were unduly affected by this variation, I ran an ANOVA to compare the projected distributions of five species currently resident in the Sahel region (addax, red-fronted gazelle [*Eudorcas rufifrons*], dorcas gazelle, slender-horned gazelle [*Gazella leptoceros*], and dama gazelle) to the other species. The ANOVA compared the proportion of projected range where only one of the species projections used to produce the ensemble model identified that area as suitable (i.e. considering all projections produced using one of the three AOGCMs). If a greater proportion of cells are only predicted by one of the three projections it suggests that one or more of the AOGCMs differ significantly from the others. Under the A1B and B1 climate scenarios there was no significant difference between the groups ($F_{(1,68)}=3.319$; $p=0.073$ and $F_{(1,68)}=1.33$; $p=0.264$ respectively), but under the A2 scenario there was a significant difference ($F_{(1,68)}=5.148$; $p=0.026$). This difference in the A2 scenario suggests that the models for the Sahel species are producing greater variability, and therefore uncertainty.

Models predicting range change between present and 2080 based on the envelope approach							
Climate scenario	Predictive model variable	variable p=	variable +/-	Significant	model R^2	model p=	Habitat filter application
A2	Optimal hottest temperature	1.25E-05	+	***	0.432	p<0.001	Off
	Optimal coldest temperature	0.049	+	*			
	IUCN Threat	7.47E-07	-	***			
A2	Optimal hottest temperature	6.90E-05	+	***	0.436	p<0.001	On
	IUCN Threat	5.22E-07	-	***			
A1B	Optimal hottest temperature	2.96E-05	+	***	0.391	p<0.001	Off
	Optimal coldest temperature	0.087	+	.			
	IUCN Threat	1.96E-06	-	***			
A1B	Optimal hottest temperature	1.89E-04	+	***	0.384	p<0.001	On
	IUCN Threat	2.37E-04	-	***			
B1	Optimal hottest temperature	4.96E-06	+	***	0.375	p<0.001	Off
	IUCN Threat	5.13E-06	-	***			
B1	Optimal hottest temperature	6.37E-05	+	***	0.354	p<0.001	On
	IUCN Threat	1.27E-06	-	***			

Table 4-6: Stepwise produced models providing the most parsimonious model for predicting range change between present and 2085 based on the envelope approach. Six models are displayed incorporating three climate scenarios and the habitat filter application (on/off). N=72 in all models.

Models predicting range change between present and 2080 based on the pessimistic approach							
Climate scenario	Predictive model variable	variable p=	variable +/-	Significant	model R^2	model p=	Habitat filter application
A2	Optimal hottest temperature	0.033	+	*	0.216	<0.001	Off
	IUCN Threat	2.93E-05	-	***			
A2	Optimal hottest temperature	0.041	+	*	0.198	<0.001	On
	IUCN Threat	6.36E-04	-	***			
A1B	Optimal hottest temperature	0.042	+	*	0.214	<0.001	Off
	IUCN Threat	9.35E-06	-	***			
A1B	Optimal hottest temperature	0.046	+	*	0.207	<0.001	On
	IUCN Threat	1.45E-05	-	***			
B1	Optimal hottest temperature	0.067	+	.	0.187	<0.001	Off
	IUCN Threat	1.18E-04	-	***			
B1	Optimal hottest temperature	0.088	+	.	0.174	=0.001	On
	IUCN Threat	1.35E-04	-	***			

Table 4-7: Stepwise produced models providing the most parsimonious model for predicting range change between present and 2085 based on the pessimistic approach. Six models are displayed incorporating three climate scenarios and the habitat filter application (on/off). N=72 in all models.

Models predicting range change between present and 2080 based on the optimistic approach							
Climate scenario	Predictive model variable	variable p=	variable +/-	Significant	model R^2	model p=	Habitat filter application
A2	Global Range	0.059	-	.	0.003	**=0.634**	Off
A2	Stepwise progression returned intercept model only						On
A1B	Global Range	0.006	-	**	0.059	=0.037	Off
A1B	Stepwise progression returned intercept model only						On
B1	Global Range	0.002	-	**	0.105	=0.019	Off
	Optimal hottest temperature	0.141	+				
B1	Stepwise progression returned intercept model only						On

Table 4-8: Stepwise produced models providing the most parsimonious model for predicting range change between present and 2085 based on the optimistic approach. Six models are displayed incorporating three climate scenarios and the habitat filter application (on/off). **Bold** "model p=" values indicate non-significant results. N=72 in all models.

Summary of the average change in climate conditions between present and 2080 average of all climate models.
Values represent the average change divided by the range of existing temperatures

	Climate variable	Hottest temperature			Coldest Temperature			Annual Precipitation		
	Climate scenario	A1B	A2	B1	A1B	A2	B1	A1B	A2	B1
Average change	Minimum	-0.214	-0.205	-0.238	-0.159	-0.139	-0.215	-0.094	-0.110	-0.110
	Mean	0.092	0.105	0.077	0.095	0.111	0.026	0.007	0.012	0.004
	Maximum	0.207	0.222	0.194	0.227	0.234	0.149	0.222	0.262	0.218
	Standard deviation	0.020	0.022	0.019	0.016	0.018	0.016	0.026	0.030	0.019

Table 4-9: The average change in climate variables by climate scenario from present day conditions to 2080. The values represent the mean, minimum, maximum, and standard deviation of the percentage change in conditions between present and 2080, divided by the range in existing conditions, where 2080 is an average of the three AOGCM predictions, e.g. (((Hottest temperature HADCM3 A1B+ hottest temperature CCSM3 A1B+ hottest temperature BCM2 A1B)/3)-present day hottest temperature)/range in hottest temperature for the present day)

Niche breadth and position

The OMI analysis shows two principal components analysis (PCA) axes account for 92% of the variation when separating species niches (Table 4-10 & Figure 4-8). These two axes were selected from the three produced for the high percentage of variation associated to them and because the eigen values were greater than one (Table 4-10; see Kaiser-Guttman criterion: Jackson, 1993; Foster, *et al*., 2012). The first axis shows a link between annual precipitation (positive) and hottest temperature (negative). The second axis shows a link between coldest temperature and hottest temperature.

Variable	**Axis 1**	**Axis 2**	**Axis 3**
Annual precipitation	0.937	-0.009	-0.350
Hottest temperature	-0.732	0.629	-0.264
Coldest temperature	0.622	0.752	0.217
Percentage of variation associated to axis	57.9%	33.9%	8.2%
Eigen values	1.73	1.02	0.24

Table 4-10: Correlations between environmental variables and principal components analysis axes.

Figure 4-9 shows the niche position and breadth for the first two axes. The niche breadth from PCA1 is a reliable predictor of species current range size (see Table 4-11). Both niche position on PCA1 and PCA2 are also close to significance. Reformulating the model to leave the most significant predictor (niche breadth on PCA1) produced similar results ($p<0.001$; $R^2=0.356$). A positive relationship with niche breadth on PCA1 suggests that species tolerating variable levels of precipitation have larger ranges. Figure 4-10 illustrates the relationship between niche breadth and current range for all species. Threatened, near-threatened, and the data deficient species are highlighted.

When niche position and breadth are used as predictive variables for the change in range size (i.e. average range remaining), this niche breadth relationship on PCA1 remains highly significant for all envelope and pessimistic approach results ($p<0.001$ in all models). In addition, under the envelope approach the position of niche on axis 2 is highly significant. This indicates that species found in warmer conditions (both hottest and coldest temperatures) perform better agreeing with the results obtained using the envelope and pessimistic approach to model range change conditions (Table 4-6).

	Coefficient	SE	t value	p value
Intercept	5.564	0.434	12.824	<0.001
Axis 1 niche position	0.491	0.260	1.886	0.064
Axis 1 niche breadth	12.197	2.057	5.930	<0.001
Axis 2 niche position	0.402	0.205	1.964	0.054
Axis 2 niche breadth	0.220	0.606	0.363	0.718
Model	adj-R^2 = 0.392; p<0.0001			

Table 4-11: Linear model predicting the range size of species as a function of their niche position and breadth on the main two axes of the OMI analysis.

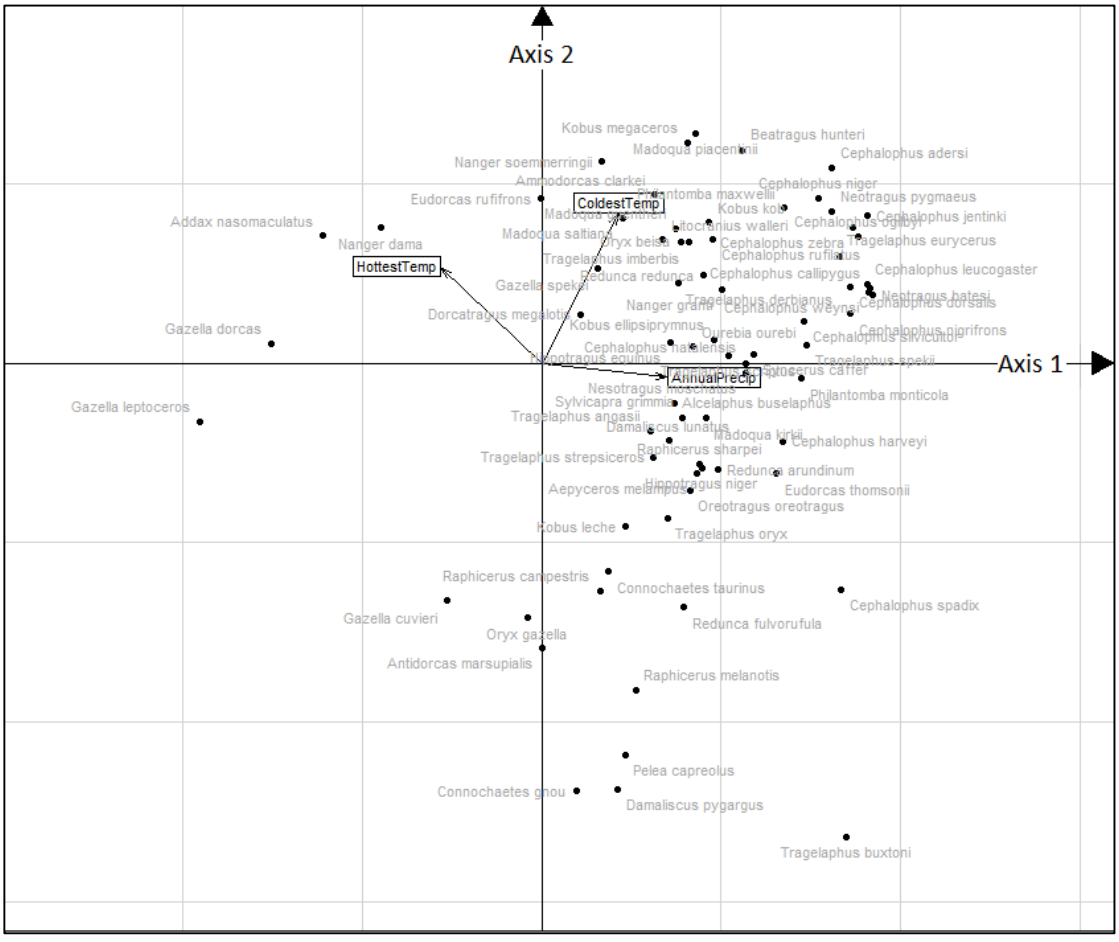

Figure 4-8: Species within the environmental niche space. The first axis (horizontal) is strongly positively linked to annual precipitation (AnnualPrecip), and negatively to hottest temperature (HottestTemp). The second axis (vertical) is linked positively to coldest temperature (ColdestTemp) and hottest temperature within the areas the species are found (see Table 4-10).

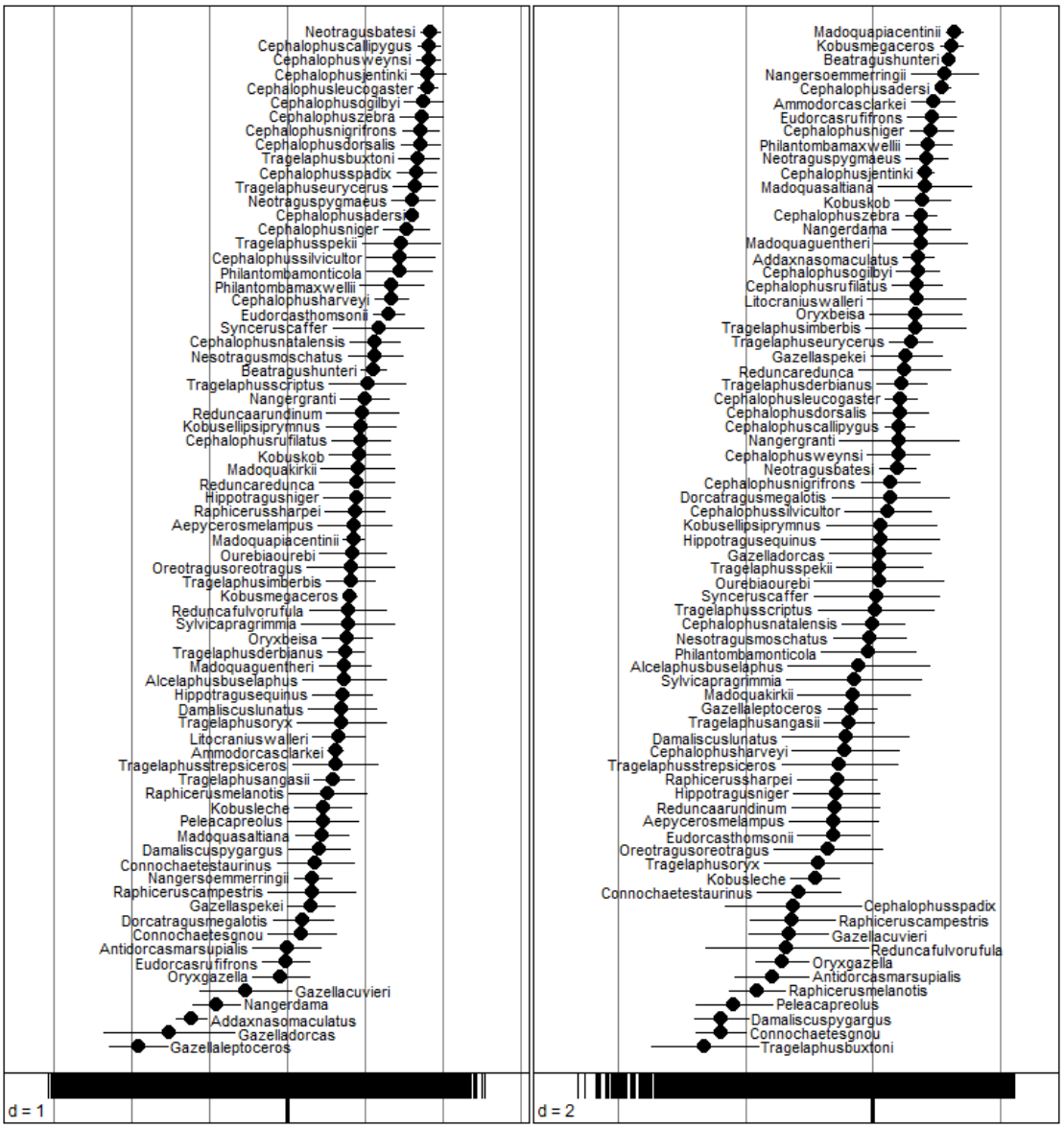

Figure 4-9: Niche position (filled circle) and breadth (horizontal lines) for the first two axes (axis one left; axis two right) based on OMI analysis of species current distributions. The bold vertical line in the bottom panels indicates the mean for the area. Species found further removed from the mean and with reduced breadth indicate specialist species.

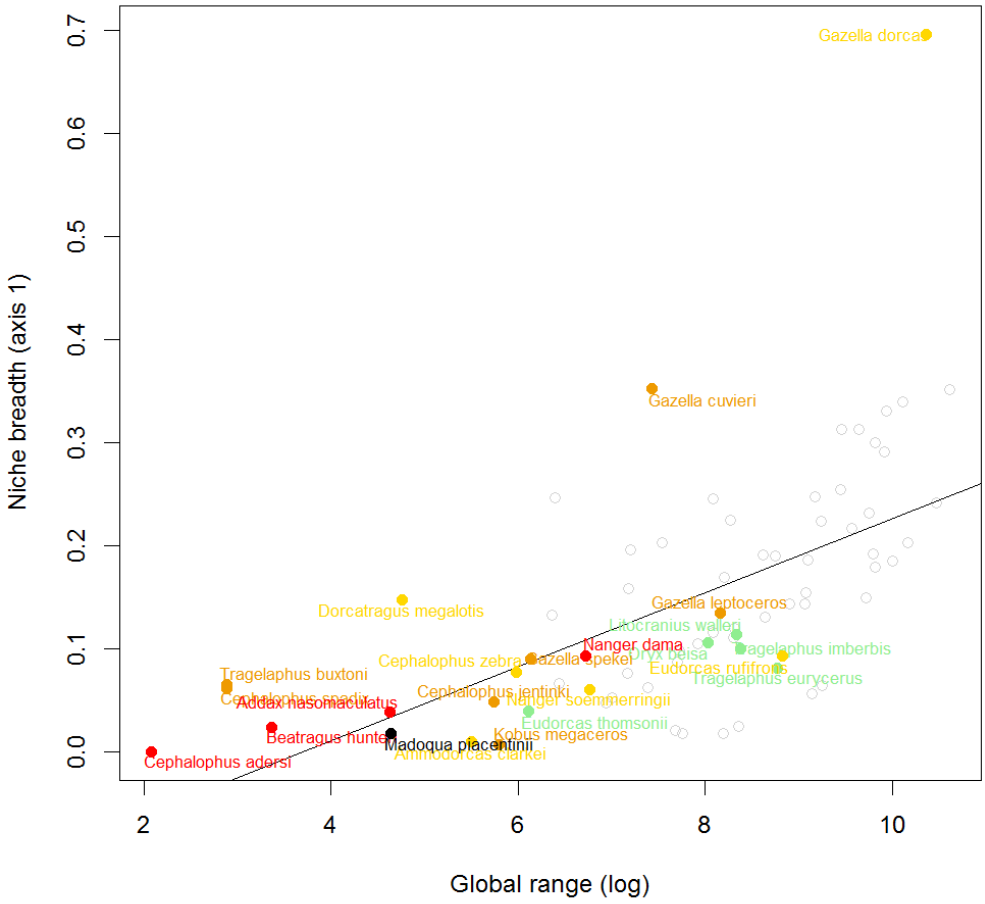

Figure 4-10: The relationship between species niche breadth on PCA1 of OMI analysis and global range. Threatened (critically endangered: red; endangered: orange; vulnerable: yellow), near threatened (green), and data deficient species (black) are highlighted. Grey circles represent currently unthreatened species. Based on the model including niche breadth and position for axis 1 & 2 (see Table 4-11).

Discussion

The models of future distributions of Africa's antelopes based on climatic variables identified worrying trends for those species already threatened and those with preferences for colder conditions. Using ensemble models incorporating three climate models, I predicted the distributions based on three climate scenarios, and three approaches. The three approaches provide predictions based on different levels of human impact (pessimistic and optimistic approaches), and potential suitable habitat (envelope approach). The results from the envelope and pessimistic approach consistently show that species which are already threatened are disproportionately affected by climate change. The relationship is not present under the optimistic approach; however, a weak relationship indicates that species with a smaller global range have a greater reduction in range in the A1B and B1 climate

scenarios. Up to six species are predicted to have no suitable range in the future under the A2 climate scenario and indicates the potential extinction of these species. One of these six, the critically endangered hirola, has no suitable range under any scenario or approach.

The envelope modelling approach is indicative of suitable conditions for a species based purely on a climate envelope model (Mbogga *et al.*, 2010; Hijmans & Graham, 2006) with a weighted land transformation filter applied. The only additional limitations here are that climatically suitable areas must have connectivity to an area that the species currently occupies. Therefore this approach models the areas of climatic suitability where the species could be present if unhindered by increased human disturbance, exploitation, and habitat loss (without the habitat filter applied). The results indicate that there is a decline in suitable areas for over 80% of species. The average contraction in range of 42%, and 19 species experiencing greater than 50% contraction (A1B climate scenario), highlights a worrying outlook for many antelopes based purely on climate. The predicted loss of all climatically suitable areas for the hirola and Aders' duiker is also a grave concern.

The pessimistic approach provides an intentionally negative outlook for species as it may be argued that conservation should err on the side of caution. The limitation for this approach is that a species cannot disperse outside its current range and models a future where human pressure of the species is approximately equal to the present day. This in itself may be optimistic given Africa's increasing population (United Nations, 2014; Boko *et al.*, 2007). The most pessimistic climate scenario (A2) linked with this pessimistic approach results in six species (addax, Aders' duiker, dama gazelle, dibatag, hirola, and Nile lechwe) having a complete loss of range, and the silver dik-dik losing 99% of its range, by the 2080 time period. The six species are all threatened, with four (addax, Aders' duiker, dama gazelle, and hirola) currently classified as critically endangered, the Nile lechwe endangered, and the dibatag vulnerable, reinforcing the concerns above that threatened species are disproportionately affected.

The optimistic approach provides a contrast to the other approaches by modelling species dispersal, where large species are able to disperse more rapidly than small. It assumes a relaxation of human pressures and seeks to provide understanding on how different species may track climate change, and the potential for conservation friendly management to improve conservation status. It differs from the envelope approach in that the starting position is the IUCN distribution rather than the model predictions based on the current climate. Species' ranges, that have been restricted due to factors other than climate, for

example human caused habitat loss or overexploitation, have the potential to reclaim those areas under this approach. This results in predictions of up to 44 species having an expansion in range compared with a maximum of 14 under the envelope approach. Furthermore, under the optimistic approach the average range remaining (ARR) is ~141% (mean A1B scenario with and without the habitat filter applied; see Table 4-2) compared with ~71% under the envelope approach. Comparisons between the envelope and optimistic approaches suggest that many species are currently restricted in their distribution by non-climatic factors. With large gains exhibited by species under the optimistic approach, this suggests that this may be modelling the recovery of previously lost range due to human caused extirpation. However, under the optimistic approach up to 34 species still exhibit contraction in range (A2 climate scenario), and the hirola loses its entire range under all climate scenarios.

Climate change and antelope biodiversity: Which species are affected?

Threatened species experience disproportionate contraction

There is general agreement in the variables that best predict range change in both the envelope and pessimistic approaches. IUCN threat status is present and highly significant in all models. This is supplemented by optimal hottest temperature in the envelope approach models, but not the pessimistic. IUCN threat status is closely correlated with global range. Hence, models where IUCN threat was replaced by global range produced very similar results. The results from the envelope and pessimistic approaches support H_2 and P_2 where species with a higher threat status will be at greater risk from CC and exhibit greater range contraction. The negative relationship between contraction of range and high IUCN threat status underlines a major concern for conservationists across Africa.

Past research has indicated that extinction risk may be higher for species with small ranges (Pearson *et al.*, 2014), however, this is to be expected if all species are affected to the same degree. Small ranges typically result in relatively smaller populations and are at greater risk from demographic stochasticity, local catastrophes, slow rate of adaptation, and inbreeding (Purvis *et al.*, 2000). Others have identified that smaller ranged species are more likely to exhibit range contractions based on historic evidence (Botts *et al.*, 2013). Furthermore, Thuiller *et al.* (2005a) concluded that rare plant species exposed to climate change were at greater risk due to a "steep decrease in suitable habitat"; however, this study did not account for dispersal ability or geographical distances. The direct risk of climate change for small-

ranged species has also been linked to the climatic rarity hypothesis (study included birds, plants, and butterflies) which associates small-ranged species with unusual climates that are more likely to be lost due to CC (Ohlemüller *et al.*, 2008). Species found in rare climatic conditions, and therefore small ranges, will similarly have a narrow climatic niche, and increased risk from climate change (Botts *et al.*, 2013; Thuiller *et al.*, 2005a). The results presented here provide evidence of a similar trend where Africa's threatened antelopes, with narrow niches, have a disproportionate reduction in range due to CC.

A narrow climate niche results in small ranged species having a narrower band of climatic conditions where they can survive. As climate changes for any variable (i.e. temperature or precipitation) it is more likely to result in unsuitable conditions for a species with a narrow niche compared to a species with a broad niche. As climate change presents warmer conditions, this may adversely affect species with preferences for cooler conditions (Thuiller *et al.*, 2005a). The findings here suggest that species with greater niche breadth in PCA1, related to precipitation and hottest temperature, will perform better in the future under the envelope and pessimistic approaches. Africa has large areas of very hot temperatures found in the deserts. The desert areas have fewer species with generally smaller ranges than those found in other areas. As the climatic conditions change a species with a narrow climate envelope is less likely to have connectivity to areas with suitable conditions or be able to persist in current areas because of its narrow climate envelope. Assuming there are no non-climatic reasons for a species' range being reduced, then small ranged, narrow niched species are more threatened by climate change.

The GLM models are based on the species' current distribution and cannot account for species specific external factors, such as human interference, unless data are available. In most cases these data are not available with the spatial references for inclusion in the models. Therefore, species heavily impacted by humans may be modelled to have narrower climate envelopes than in reality. However, a reduced range will still often be representative of a species' climatic envelope. In these cases a species' predicted range may be far greater than the actual range. When these predictions are compared with details of a species' historic range, it is common to see that there are significant areas of overlap. For example, Figure 4-11 illustrates (a) the distribution of Aders' duiker, and (b) the model predictions of climatically suitable areas. This appears to suggest a poor model representation, however, the species is reported as previously being widespread in forests, woodlands, and thickets in coastal regions ranging north from its current distribution (Finnie, 2008). Recently, the

species has been located in areas close to Somalia, and suitable habitat may be present in forests across the border (Andanje *et al.*, 2011). Historically, a narrow strip of coastal forest stretched along the east coast of Africa from Somalia to the Aders' duiker's existing mainland distribution in the Arabuko-Sokoke forest in Kenya (Oyugi *et al.*, 2007). Deforestation and hunting has resulted in Aders' duiker now being found only in Zanzibar and in the remaining parts of Arabuko-Sokoke forest, the last remaining areas of lowland forest on the East African coast (Finnie, 2008). This is a great concern for the species, but suggests that the model, based on very few data points, represents the climatological restrictions of the species. Further north in Somalia the habitat has been transformed to croplands (USGS, 1999); it is unclear if this area was previously suitable for Aders' duiker.

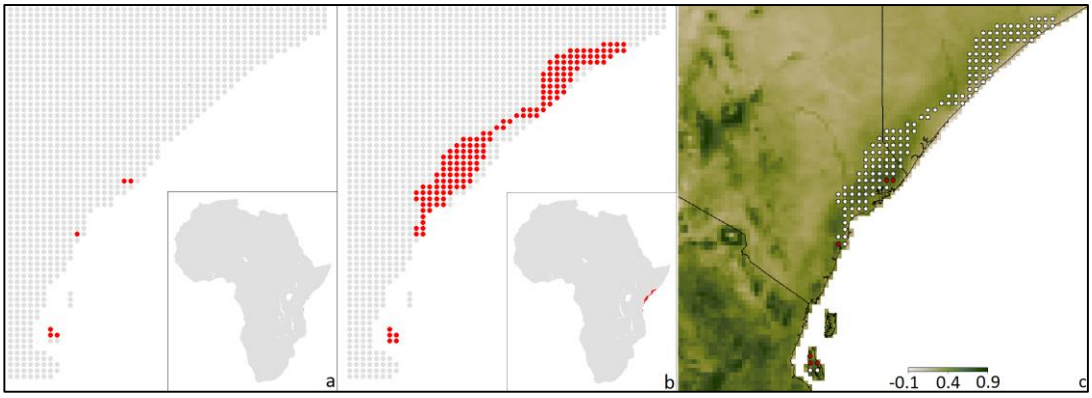

*Figure 4-11: a - current distribution of Aders' duiker (*Cephalophus adersi*). b – the predicted distribution of Aders' duiker based on the climatic model, without the habitat filter applied. c – both predicted and current distributions with normalized difference vegetation index (NDVI) shading for December 2014 (1 month) (NASA, 2015). Darker green indicates denser vegetation and forest areas (Meneses-Tovar, 2011).*

The Aders' duiker model supports the use of the envelope approach as a means of identifying suitable areas both now and in the future if species were not affected by human impact. It suggests that while there may be some limitations in the accuracy of models for species with small range due to human activities, those models are still broadly representing the climate preferences of the species.

Hottest temperature preferences predict range change

The envelope models demonstrate a positive relationship between optimal hottest temperature and projected range change. Therefore species with higher optimal temperatures are forecast to perform better in light of global warming trends which supports H_1. This is also reflected in PCA2 which indicates that warmer coldest and hottest temperature preferences are important in determining larger current range size, and indicate greater expansion, or reduced contraction, of range in the future.

Through the stepwise model selection optimal hottest temperature is retained, but is not significant in one optimistic and three of the six pessimistic models. There are two main differences between the envelope approach and both pessimistic and optimistic approaches that may explain the weaker relationship to hottest temperature found in the latter; (i) the starting point and, (ii) dispersal ability. As discussed above, the envelope approach may have a larger starting range than the IUCN distribution as the current distribution is predicted based on the species' model. Therefore, under the envelope approach, providing there is connectivity between the predicted current distribution and future conditions, all future suitable conditions will be encompassed as there is no dispersal limitation. As CC is expected to raise temperatures this results in species, with a climatic envelope that encompasses hotter temperatures, predictably increasing. The pessimistic approach does not allow dispersal so any change in climate will lead to a loss of range when the conditions shift beyond their climatic niche. In this case species with broader climatic envelopes should perform better and vice versa. This agrees with the findings of Thuiller *et al*. (2005a) who found that plant species with smaller distributions and narrower niche breadth performed worse.

Significance of rainfall in explaining range change - expected but not detected

Previous research has demonstrated the importance of precipitation in understanding the distribution and biomass of antelopes and other African species (Hopcraft *et al.*, 2009; Ogutu & Owen-Smith, 2003; East, 1984; Coe *et al.*, 1976). This was further demonstrated in the production of the models used here and the importance of precipitation explained in chapter three. Precipitation was also highlighted as an important component of axis one in the niche analysis. However, it was not found to be a significant variable when predicting range change in the future under any approach. There are a number of possible explanations for this which are discussed below.

Precipitation does not have the same scale of change between present conditions and 2080 compared to the two temperature variables (see Table 4-9). In general, temperature exhibits continent-wide increases, with latitudinal differences, whereas precipitation exhibits positive and negative changes, typically on a regional basis, but also with longitudinal variation across the tropics generally increasing towards the west. It is therefore understandable that temperature, as the more consistent variable, will provide a more consistent predictor than one that is inconsistent. The reduced scale, and spatial changes, in projected precipitation are also consistent with the changes experienced in the past

century (1900-2000), during which temperatures generally rose while precipitation changed on a more regional basis (Hulme *et al.*, 2001).

Uncertainty about the magnitude and directional change over the 21st century is also greater for precipitation than for temperature (Hulme *et al.*, 2001) as shown by the three AOGCMs used to produce the species projections. This is the source of the greater variation displayed in the change in precipitation compared to the coldest temperature variable. There are currently limitations on the modelling of important precipitation mechanisms such as the hydrological cycle, orographic precipitation (precipitation caused by upwards airflow due to mountain deflection or daytime heating), sea-surface temperature anomalies, deforestation, and soil moisture (Hulme *et al.*, 2001; Boko *et al.*, 2007). The area of greatest debate is the western Sahel region (approximately 10°N to 18°N, 17.5°W to 20°E) which has experienced large reductions in rainfall since 1950 that some attribute to human caused deforestation (Odada & Olago, 2005). Uncertainty results in some models predicting drying whilst others suggest wetting with expansion of vegetation into the Sahara. Further uncertainty is found in relation to the tropical zone of Africa with some models predicting drying in the west while others suggest wetting, but most agree that increased precipitation will be seen in the east of this area (Malhi *et al.*, 2013). There are general trends for Africa though: drying along the Mediterranean coast and northern Sahara; drying in southern Africa during the winter (June to August) which is already a dry period; and increased rainfall in the tropics and eastern Africa although there are differences in the equatorial regions by latitude and longitude (Boko *et al.*, 2007). The three climate models used to produce the ensemble forecasts agree on the general precipitation patterns for southern Africa, albeit in different magnitudes. However, differences are found in the Sahel region. The HADCM3 climate model has drying to the west and north of the Sahel region, and wetting in an area around the Tibesti mountains. The CCSM3 climate model has drying in the far west, but a band of wetting at approximately 20°N starting at 3°W and spreading east to the Red Sea. The BCM2 climate model has a similar pattern to CCSM3 with a band of wetting approximately at 20°N, but starting at 5°E and spreading east to the Red Sea. However, the BCM2 model also predicts an area of drying directly south of this band not seen in CCSM3. Such variations in predictions may therefore cause confusion across a number of models thereby reducing the influence of precipitation as a predictive variable. Species currently found in the Sahel region may therefore be adversely affected by these differences.

Climatic divergence as a driver of range loss

The differences in the spatial nature of change between climatic variables, where temperatures may change latitudinally compared to precipitation that changes regionally/longitudinally, presents the potential for the divergence of climates within Africa. The difference in the scale and direction (i.e. increase or decrease) of these changes may also influence divergence. For example, if suitable temperatures for a species move southwards, but suitable precipitation moves east, the suitable climatic conditions are found to be diverging in different directions. Below I introduce the hirola as an example of how climatic divergence is predicted to affect species under different climate model predictions.

The hirola (*Beatragus hunteri*) is predicted to have a 100% contraction of range in all modelling approaches, across all climate scenarios, and irrespective of the habitat filter. The species loses its entire range by the 2055 time period with greatly reduced range by the 2030 period. The critically endangered hirola is already considered one of the most threatened antelope in Africa. The decline in population is attributed to hunting, disease, drought, competition with livestock, and habitat loss. In addition, the status of species in Somalia is unclear due to prolonged military and civil upheaval (IUCN SSC Antelope Specialist Group, 2008a). What makes this species prone to the effects of climate change is therefore important to understand in order to devise mitigation strategies, which could also be relevant to other taxa with similar characteristics.

The original predictive model closely matches the existing distribution and includes areas of southern Somalia, suggesting that the model is correctly identifying the species climatic needs (AUC=0.9996). The hirola is found in an area with a relatively small range in temperatures (minimum temperature 19.8-21.1°C; maximum temperature 33-36.3°C) and a small range in precipitation (403-659mm/year). The three climate models offer different predictions for the area with such climatic conditions. Below I explain the changes predicted by each climate model for the hirola's range in 2030. Currently, the hirola range has opposing gradients in temperature variables, i.e. the warmest hottest diurnal temperatures are in the northwest of the range, and the warmer coldest temperatures are in the east and south nearer the coast. There is greater rainfall in the south than the north within the hirola's existing range.

a) The CCSM3 model projections have increases in the coldest temperature and, depending on the climate scenario, variable cooling and heating for the hottest temperature. The CCSM3 temperature projections have larger changes than the

other climate models and this results in no area within the current range providing suitable conditions and no neighbouring areas for dispersal in 2030. Precipitation remains relatively stable during this period under this climate model.

b) In the HADCM3 projections a general increase is seen in all climate variables. Precipitation increases are greater to the north and inland, while hottest temperature increases are greater in the south. Due to the different existing gradients, this results in suitable temperatures moving southwards while suitable precipitation levels move northwards and inland. Temperatures change at a faster rate than precipitation resulting in a contraction of range with suitable conditions confined to the south. By 2055 this divergence of conditions results in no suitable areas for the hirola, even with the unlimited dispersal under the envelope approach.

c) Only in the BCM2 models does the hirola disperse and only in 2030 under the optimistic approach. This occurs to the south of its range and is due to the largely stable conditions in this area based on this climate model. This suggests those areas are currently climatically suitable, but that the hirola is not present due to other factors. However, the 2055 period presents a similar scenario to the HADCM3 projections with a rapid divergence in climate conditions and no suitable areas being available.

For the hirola there is a divergence from the climatic conditions preferred by the species. The climatic changes predicted for Africa suggest this may also affect many other species. My *a priori* assumption was that a species' optimal climatic conditions would shift, but remain largely consistent on a continent-wide scale except for coastal species. That being the case a species would need to track the changes. However, climatic change is not consistent, particularly in Africa where precipitation relies on so many processes (Boko *et al.*, 2007; Hulme *et al.*, 2001). As noted above, predictions of temperature exhibit latitudinal changes, whereas precipitation changes, despite having a longitudinal trend, are more regional and less consistent between climate models (see Hulme *et al.,* 2001). Thus, the results from different AOGCMs result in differing regional precipitation projections as highlighted above (also Hulme *et al*., 2005), whereas temperature experiences a more general increase. The result is likely to be a climatic divergence reducing the suitable area within a species' climatic envelope. Climatic divergence results in the loss of climates and the assembly of novel climates (i.e. new combinations of climatic conditions not experienced at present). Previous studies have suggested that this is particularly relevant for tropical areas including Africa (Williams *et al.*, 2007).

Ecological and morphological variables

There were no significant relationships between morphological or ecological variables, but this does not discount the possibility of a relationship with other untested variables. P_4 predicted that the size of a species would influence the ability to disperse and therefore augment the possible range increase in the future. This was hypothesized to affect the optimistic approach results due to influence of dispersal ability, rather than the envelope approach where dispersal was unlimited. However, this was not the case: body mass, shoulder height, and shoulder to horn ratio all proved non-significant in all models predicting range change. Further to this, analysis of the unfulfilled grid cells showed no significant correlations with any of the species morphological traits.

It was hypothesized that specialist species would be less able to exploit areas of climatic suitability in the future due to dispersal limitations (H_3). P_3 predicted that habitat generalists would be able to expand their range to a greater degree than open/closed habitat specialists when the habitat filter was applied to the optimistic approach, due to habitat barriers; however, this was not the case and H_3 is rejected. The habitat filter has little effect on specialist species ability to expand their range although there are individual exceptions such as Aders' duiker. This is due to the largely heterogeneous nature of habitat in Africa whereby open and closed habitat routes are available to species which allows them to disperse. In the future, with greater knowledge of species habitat preferences, it may be possible to produce finer scale filters that further restrict species to certain vegetation/habitat types. This would be likely to reveal a greater impact on species dispersal than the open/closed filter presented here.

Modelling techniques: Do they capture reality?

Ensemble models increase confidence in species distribution predictions

The reason for using ensemble models incorporating multiple AOGCMs is that climatic predictions do not always agree on the future patterns of change (Fordham *et al.*, 2012). In respect to temperature there is general agreement between the three that warming is reduced in coastal areas. However, the pattern of inland changes varies. The HADCM3 model used here agrees largely with the latitudinal temperature changes reported in Boko *et al*. (2007), where temperatures will rise 3-4°C by 2080-2099 (under the A1B scenario), with less warming in coastal and equatorial areas. The CCSM3 model also largely agrees with

Boko *et al*., but the B1 scenario demonstrates a higher degree of warming at high latitudes. Finally, the BCM2 models display more warming in the southern hemisphere and more warming of the tropics than seen in the other two climate models.

In addition to the differences in predicted precipitation described above there are variations in the temperature predictions. These differences highlight the importance of using ensemble modelling to gain a more rounded view of the impact of climate change on species distributions. The differences found in the changes of species ranges between models within the same scenario (Table 4-5) highlights the need for the ensemble model methodology. Fordham *et al.,* (2012) advocate the use of averaged values from multiple AOGCMs simulations as these provide strengthened forecasts. However, by averaging values, outliers may adversely affect predictions based on those averages. As an alternative, the AOGCM responsible for the outliers can be removed entirely from the ensemble (Fordham *et al.*, 2011). This method is in contrast to the ensemble models here, where three species distribution predictions are made based on the three AOGCMs for each climate scenario. Here, the ensemble modelling technique accepts a consensus agreement of multiple projections rather than basing all projections on an average value. Therefore, I believe the ensemble models increase our confidence in the areas predicted as climatically suitable for each species. Hence, when planning protected area networks it seems prudent to only focus on those areas where multiple predictions agree.

Temporal resolution could limit dispersal ability for species with narrow niches

It is possible that the temporal resolution (20/30 year climate periods) could also affect dispersal potential. Climatic windows are commonly considered as 30 year windows to eliminate year-on-year variability (Met Office, 2012). However, this could cause a bias in terms of dispersal of small ranged species or species with a narrow climate envelope. For example, the difference in climatic conditions between the present day and the 2030 climate window could potentially be far greater than if a 10 year temporal scale was used. This could affect species with narrow climate envelopes as areas of suitable conditions could appear to be beyond the reach of those species where a finer temporal resolution would enable them to track the climate. However, as previously noted, climatic change is variable and therefore large shifts can also occur rapidly. Therefore there is an argument to suggest that using coarser temporal resolution accommodates the possibility of rapid shifts in climatic change.

Habitat change versus climatic change

The habitat filter, whilst not significant for most species, was applied to provide understanding of how open and closed habitat might affect a species' ability to disperse. The use of "open" and "closed" categories in preference to a more species specific habitat requirement, was due to the high heterogeneity of habitats found for many species based on their current distributions and the USGS (USGS, 1999) data sets. If it were possible in the future to further link species to a habitat type then the habitat filter may have a greater influence on the results.

Here, dispersal pace is calculated based on body mass (Schloss *et al.*, 2012) which is an oversimplification. This method does not take life history, social structure, density of distribution, inter- and intra-specific competition into account, but at present there are too few antelope specific data to build a more robust model. The habitat filter also relies on the assumption that habitat will remain static over the next century. This is clearly a large assumption, plants disperse as do animals, but they are not expected to disperse in pace with climate (Corlett & Westcott, 2013). In addition, CO_2 and climatic changes are likely to benefit some plant species more than others. The rise in CO_2 will benefit trees over grassland which has already been seen in studies that demonstrate areas where woody encroachment is occurring. Changes show encroachment into savannah areas as well as woody savannahs becoming woodier (Mitchard & Flintrop, 2013). Vegetation models provide similar results with forest expansion driven by CO_2 rather than climate (Huntingford *et al.*, 2013; Moncrieff *et al.*, 2013). Evidence from satellite images (1982-2006) shows increases in 4.0% of Africa's non-rainforest woody vegetation, and decreases of 3.5% in range. The decrease is not attributable to changing CO_2 levels; rather it is linked to human degradation through agriculture and fuel use (Mitchard & Flintrop, 2013). Therefore the prognosis for closed habitat specialists is complex.

Until further projections can be made for Africa at a fine scale (such as van Breugel *et al*., 2011) there appears little advantage in employing the current habitat filter as the results are not significantly different. However, there are individual species, such as Aders' duiker, where the filter highlights important species specific problems related to human caused habitat degradation. The areas surrounding Aders' duiker's current range are largely incompatible with the species' needs as they are open rather than closed. In the field, Aders' duiker face multiple threats. In Kenya, hunting significantly threatens the existence of this species. Over-hunting is also occurring on Zanzibar, however, large scale deforestation is

considered the main threat to this population. The Arabuko-Sokoke forest in Kenya is one of the last remaining areas of lowland forest on the East African coast and fragmentation is reflected in the species' current reduced distribution (Finnie, 2008). In this circumstance the static habitat filter functions well as it is unlikely that the surrounding areas will be subject to habitat restoration.

New and existing climate scenarios, and the opportunity to expand ensemble modelling

The present set of IPCC climate scenarios provides a wide range of futures. From the IPCC scenarios used here A2 is considered the worst case scenario with continually increasing greenhouse emissions. The A1B (balanced) scenario, has a strong rise in CO_2 emissions before a reduction after the middle of the century, while B1 has a relatively slow increase in comparison. The B1 presents confusion because Averaging Range Remaining-values for this scenario are generally below those of A1B. The reason for this is that the CCSM3 B1 projections include localized high hottest temperatures while the precipitation and coldest temperatures are in line with the B1 scenarios for other projections. The result of this is that the CCSM3 B1 species projections are restrictive which in turn has led to lower range estimates in extent even if these are based on two of the three models. The same localized patterns in hottest temperature does not apply to the A1B and A2 scenarios.

It is unclear which scenario best represents the future. Recent data suggest that the worst case scenarios (A2, and A1F) are currently being followed or exceeded (Peters *et al.*, 2013), but there is potential for technological breakthroughs that will greatly reduce emissions. It is therefore prudent to continue with a number of scenarios. The most recent IPCC report has replaced the climate scenarios with new Representative Concentration Pathways (RCPs) which should now be used for future studies (IPCC, 2013b). These are representative of the most recent greenhouse gas projections. Additional climate model projections utilizing the RCPs are now becoming available which enables a more comprehensive ensemble modelling and lessens the potential impact of a single model as in this study.

Lower risk species and taking positive steps in planning for the future

No patterns identified for lower risk species

The results also highlighted species that consistently performed well in terms of range expansion (or least contraction for the pessimistic approach). Beyond the general predictive variables found for all species, there are no significant relationships between these species in terms of ecology or morphology. Still, patterns were present in that those species that perform well in the envelope approach also tended to do so in the pessimistic, but not in the optimistic, and vice versa. No species trait relationships were found to explain this but this may be related to the small sample size. Of note was that habitat specialists and generalists were both equally represented.

The top three species Ogilby's duiker (*Cephalophus ogilbyi*), kob (*Kobus kob*), and bohor reedbuck (*Redunca redunca*) also have little in common except that they are dietary specialists, but with different forage types (one frugivore, two grazers). With no commonality amongst species, species specific factors should be considered to explain why certain species perform well or poorly.

Identification of species at risk is the first step in conservation planning

A study such as this can result in great negativity and pessimism for the species at hand and the future in general. However, while this research identifies species at risk from climate change there are positive messages to take. By identifying species at risk we are able to better plan for their future. The pessimistic approach is intentionally negative towards the future, but should be used to highlight issues that can still be addressed given the required political impetus. Indeed, under the optimistic approach species with small ranges show the potential to expand their ranges to a greater degree than larger ranged species, albeit the variance explained by the models was very low. However, this shows that given a conservation friendly future these species show the potential to be able to recover. Where new areas become available for species of conservation concern the challenge will be how to facilitate their expansion given the human pressures on resources. Chapters 5 and 6 investigate this in more detail based on the findings here.

5. Gap analysis identifies priorities for protected area network development in Africa from an antelope perspective

Abstract

In this study I investigate the effectiveness of Africa's existing protected area network in providing protection to a key group of species: the antelopes. This diverse group plays important roles in the ecosystem as an ecosystem architect and as prey species. Many antelope populations are declining, largely due to human factors such as hunting and habitat conversion, and are therefore in need of protection. Using Marxan conservation planning software, I produce protected area network solutions that protect Africa's antelopes based on their predicted distributions in 2080. Two solutions are presented based on low and high protection options and require 8.1% and 8.7% respectively of Africa's land mass in order to protect 71 species of antelopes. These solutions, that are based around the existing IUCN protected area network (categories Ia-VI), reveal key new areas are required in Somalia, while expansion of existing protected areas (PAs) are required continent-wide, particularly in Liberia, Cameroon, Kenya, Tanzania, and the Central African Republic. I also find that the contribution of non-IUCN PAs, including community led PAs, to these solutions is currently limited, but in some areas play an important role in bridging gaps between existing IUCN PAs.

Introduction

Ecosystems and their constituent species are under increasing pressure from multiple fronts as wildlife populations are in decline. Vertebrate populations show, on average, a 52% decline in size between 1970 and 2010 (WWF, 2014). During the 21st century climate change is anticipated to have a rapidly increasing impact on all ecosystems as conditions change globally (MEA, 2005). The major conservation tool used to protect against biodiversity loss is the designation of protected areas (PAs). PAs have grown exponentially over the past few decades, particularly in developing countries, with the aim of significantly reducing the rate of biodiversity decline (Naughton-Treves *et al.*, 2005). Modern-day PAs are setup to protect natural features and areas of great biodiversity value, be that high levels of diversity, endemism, or ecosystem services (Watson *et al.*, 2014). However, PAs are largely static in nature and therefore it is unclear whether they will continue to protect species in the future as ranges shift due to climate change (Araújo *et al.*, 2011). In this study I investigate the performance of Africa's protected areas in relation to the preservation of a key group of

animals: the antelopes. This diverse group of species is found throughout the continent, occupying most of its varied habitats from deserts to tropical forests to mountain regions. Building on the existing IUCN protected area network I present solutions for the extension of that network to establish adequate protection for all species in 2080. I identify species of particular concern due to climate change and lack of protection, and I specifically investigate the contribution of community based conservation areas in Kenya, Namibia, and Tanzania to antelope conservation both now and in the future.

The global protection of biodiversity holds importance at many levels from individuals to ecosystem services, from the preservation of a species to the wellbeing of humanity. How each facet of biodiversity is protected is dealt with at various political scales. These range from international organizations and conventions such as the International Union for the Conservation of Nature (IUCN), the Convention on Biological Diversity (CBD), and the Ramsar Convention on Wetlands, to continental, national, and local governmental policies and plans. In addition, small protected areas and community management can also provide conservation measures at a local level. Protection itself takes place within international, national, local legal frameworks, and multilateral agreements. Protected areas (see Box 5-1) are commonly designated on a national level where each nation has different laws and conservation objectives. Within a country, PAs can be joined to form a nation's protected area network (PAN) (Dudley *et al*, 2014), and national PANs can be joined, in a wider context, parts of a continental or worldwide PAN.

> 'A clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values'

Box 5-1: Definition of a protected area (Dudley et al., 2014).

The question of what to protect, and how much to protect is a complex issue with ongoing debate (Larsen *et al.*, 2014; Locke, 2013). Currently, over 12% of the Earth's land mass is designated as protected (Dudley *et al.*, 2014; Geldmann *et al.*, 2013). The CBD Aichi 2010 targets prescribe an increase in PAs to at least 10% of the marine and coastal areas, and for 17% of land area to be protected by 2020. New PAs are to be focused on areas of high importance to biodiversity and ecosystems services (CBD, 2010). However, the Aichi targets are set to be politically acceptable rather than scientifically driven (Larsen *et al.*, 2014). Current research suggests that the 17% land area target will be inadequate to protect biodiversity and safeguard ecosystem services (Larsen *et al.*, 2014). The 17% refers to a

global average; however, the figure will differ between countries. For example, in order to protect large herbivore populations from their continued decline Stoner *et al*. (2007) emphasize the need for more protected areas in Tanzania, a country with one of the highest protected area coverages in the world at 38.03% (World Bank, 2012).

Efficacy and performance of PAs are hard to quantify unless there are clear goals assigned to management plans for the area. How one measures the performance may vary depending on those goals. In Africa, PAs show reduced loss of natural land-cover compared with areas outside (Beresford *et al.*, 2013; Geldmann *et al.*, 2013); however, they do not consistently protect animal populations (Geldmann *et al.*, 2013; Craigie *et al.*, 2010). Craigie *et al.* (2010), also indicate that the performance of PAs varies by region with southern African PAs performing better than those in the east and west of Africa. However, Toth *et al*. (2014) describe stable or increased species richness (alpha diversity) and decreased uniqueness (beta diversity) of mammal communities in six Kenyan PAs over 100 years. Decreased uniqueness was the result of species expanding their ranges to be found in other areas, which also contributes to increased richness of those areas. While some transient species left the PAs they were replaced by others and landscape diversity (diversity across all areas; gamma diversity) remained stable. However, the same study indicates that wild grasslands continue to be converted to croplands albeit at a slower rate than outside of the PAs.

In order to secure more land for conservation, recently, community based PAs have received the focus of conservationists. Community led conservation is largely the result of a number of conservation approaches developed over recent decades, such as Community-Based Conservation (CBC), Integrated Conservation and Development Projects (ICDP) (Berkes, 2004), Community-Based Payments for Ecosystem Services (CB-PES), and Community-Based Natural Resource Management (CBNRM) (Dougill *et al.*, 2012), amongst others. These approaches often focus on one or more conservation goals such as carbon sequestration, maintaining or rehabilitation of biodiversity, or watershed preservation. Community PAs, particularly prevalent in forest communities in South America, Mexico, and parts of Africa, rely on the community adjacent to the PA taking responsibility for some or all management, monitoring, protection, and sustainable harvesting of the resources therein. The communities then benefit from development and financing from ecotourism, hunting and/or the services the PAs are providing. Studies show that where community management is in place the degradation of those areas is typically less, and less variable, than in conventionally managed PAs (Porter-Bolland *et al.*, 2012; Ellis & Porter-Bolland, 2008), however, success is

not universal (Measham & Lumbasi, 2013). This stresses the importance of recognising community PAs and understanding how they fit into the wider PAN.

Africa's community conservation is not restricted to forested areas as often seen in other parts of the world. Namibia has a strong CBNRM background with large areas of savannah under community management and fewer designated as IUCN sites. This is due to a historical legacy from the 1970s when farmers were allowed to manage wildlife on their land while realising the financial benefits of that wildlife. A multi-million dollar wildlife industry developed over time with increases in some wildlife populations, and re-emergence of lost species to some areas (Jones & Weaver, 2009). While there continues to be debate on the success of CBNRM, successful projects exist such as the hirola oriented Ishaqbini Community Conservancy in Kenya (Measham & Lumbasi, 2013).

The location of PAs within the PAN is a subject requiring careful planning if conservation goals are to be achieved. Until the 1980s conservation planning largely revolved around a species by species, or threat by threat approach within the established PAs (Scott *et al.*, 1993). However, with an increasing recognition of the global threat to biodiversity new approaches were needed. Assuming finite fiscal resources, the positioning of national or local government funded PAs must be completed in the most efficient manner whilst meeting conservation objectives such as the Aichi targets. A key tool for conservation planning in this area is 'gap analysis' which was developed in conjunction with advances in geographic information systems (GIS). Originally gap analysis used vegetation and species distribution data as indicators of biodiversity. This was then overlaid with a land use layer identifying areas that were protected. Gap analysis then finds areas which are of importance in the protection of species, i.e. "gaps in protection of biodiversity" (Scott *et al.*, 1993). The process has subsequently been comprehensively used and enhanced (Rodrigues *et al.*, 2004a; Rodrigues *et al.*, 2003; Kiester *et al.*, 1996).

An important concept currently central to gap analysis is that of 'irreplaceability'. There are many definitions for irreplaceability (Ardron *et al.*, 2010; Rodrigues *et al.*, 2004a; Pressey *et al.*, 1994), but here it is considered to be "the likelihood that it [an area] would be included in an expanded protected-area network that represented all species to their representation targets" (Rodrigues, *et al.*, 2004a). An area can thus have an irreplaceability from 0% (not required in the PAN) to 100% (a site that must be within the PAN). Irreplaceability is only calculable for small datasets. For large datasets alternative predictions or methods are used such as selection frequency (previous labelled 'summed irreplaceability') which produces

multiple rule-based solutions for conservation targets that are set. Here we use Marxan software (Ball *et al.*, 2009) to set rules for conservation priorities and costs associated with developing a PAN to produce the best solution. The rules are based on a species' percentage of range being protected within an African PAN that is based around the continent's existing IUCN PAs.

A common assumption is that PAs protect the species within them by protecting against the processes that threaten them (Araújo *et al.*, 2011). However, while this may be the case for direct threats such as exploitation, indirect threats such as climate change present a different problem. Species demonstrate natural phenological and spatial responses to climate change (Lenoir & Svenning, 2013; Hickling *et al.*, 2006; Parmesan, 2006), and predictions suggest that climate will cause greater distributional changes in the future (Pereira *et al.*, 2010; Thuiller *et al.*, 2006b). Changes in species distributions will clearly impact on the effectiveness of PAs if species disperse beyond their boundaries, however, some species may remain, and other immigrant species may replace those that disperse (see Toth *et al.*, 2014). It is common to assess the impact of climate change on species distributions using modelling techniques such as bioclimatic models (Araújo *et al.*, 2011). These models predict species distributions based on future climate projections, and allow us to better understand (a) how well species are represented by the existing PAN in the future and compare that with the present, and (b) develop PAN solutions that adequately protect species based on those predicted distributions.

This study presents analysis of the existing African PAN, and develops PAN solutions for 73 of Africa's antelope species based on each species' projected distribution in 2080. Antelopes play critical roles in the ecosystem by moulding landscapes, as seed dispersers, nutrient recyclers, and as prey species. Antelopes are also a vital source of protein for indigenous human populations. The importance of antelopes, the fact that 63% of species populations are in decline, and 23% are listed as threatened (IUCN, 2014a), indicates a group of species that are of great conservation concern. Antelopes, as with most species, face multiple threats. The existing threats include habitat loss and agricultural encroachment linked with disease, over-exploitation through hunting, and climate change (largely related to drought and habitat-loss caused by desertification and applied to arid adapted species). Africa's economic and agricultural frailties, when linked with a rapidly increasing human population that could see the population of Africa quadruple by 2100 (under a medium fertility scenario [United Nations, 2013]; see Figure 5-1), will likely have a secondary impact, that of further

exploitation of bushmeat (Lindsey *et al.*, 2013; Shackleton & Gumbo, 2010; Boko *et al.*, 2007). While PAs do not offer 100% protection from exploitation and poaching, population decline is reduced within them (WWF, 2014) and anti-poaching efforts have delivered increases in ungulate populations (Geldmann *et al.*, 2013), clearly demonstrating the importance of these areas.

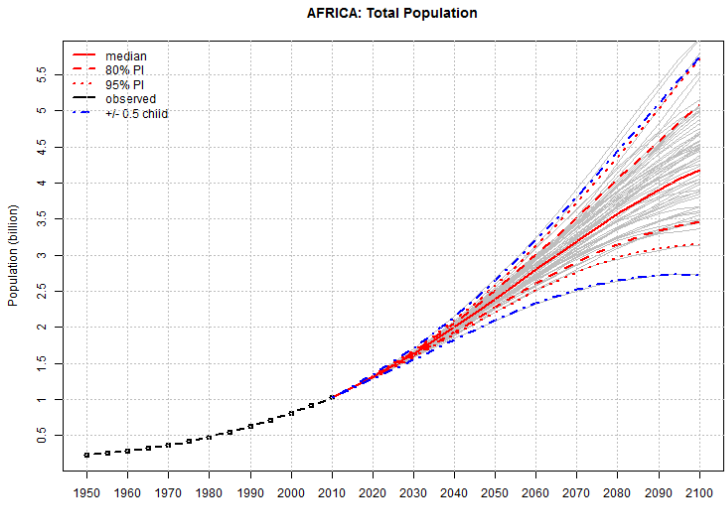

Figure 5-1: Africa's population growth estimates in the 21st century showing a median potential population of over 4 billion derived from multiple scenarios (United Nations, 2014).

Two of the three predictive approaches of antelope distributions presented in chapter four are used here to analyse and compare how well the existing PAN protects current and future (2080) ranges. The first of the two approaches takes a 'pessimistic' view of the future where the species are unable to disperse from their present range. This causes a contraction of range based on the climate requirements of the species and is suggestive of a future where human pressures continue to increase on all species. The second approach is based on areas of climatic suitability (labelled the 'envelope' approach). This prediction takes climatically suitable areas connected to the present distribution and projects these into the future, assuming connectivity through three time periods (2030, 2055, and 2080). This approach provides a view of all areas in which the species could potentially be present given no limit on dispersal. This is indicative of where a species might be found in a world without human interference, borders, fences, or hunting pressure. The pessimistic and envelope approaches were chosen as they present two extreme scenarios for species, one is highly restrictive and the other is indicative of the conservation potential under intensive management. Therefore, the envelope approach helps us identify areas for the future that may be suitable for translocation if natural dispersal is not possible, and it presents more options than the

optimistic approach (not used here, see chapter four) that restricted dispersal based on body mass.

The analysis aims to demonstrate how the existing PAN protects species in the future compared to the present based on the percentage coverage of range and the absolute number of grid cells within PAs where the species are present. The Marxan software is used to create two PAN solutions that protect a percentage of each species' future range taking the present IUCN PAN as a starting point. The target percentage of range to be protected for each species is set to depend on its absolute range to ensure that species with limited ranges have greater protection than those with wide ranges. This follows the findings from chapter three whereby wide ranged species are less threatened than limited range species. The two PAN solutions are based on a low and high protection requirement where the high protection status protects a greater percentage of species' range than the low. To establish the significance of CBNRM, three countries' data were extracted from the main dataset for further examination, i.e. Kenya, Namibia, and Tanzania, as community PAs could be identified as a subset of non-IUCN PAs for these countries.

The aim of this study is thus two-fold. Firstly, I investigate and identify the level of protection being afforded to each antelope species by the existing African PAN. This includes analysis of IUCN versus non-IUCN PAs for Africa and a further subdivision of community managed PAs for the country specific analysis where the data is available. Secondly, I seek to identify a PAN solution that efficiently protects all antelope species according to the set requirements based on the existing IUCN PAN.

Methodology

This chapter uses the A1B climate scenario ensemble predictions for 2080 that were produced in chapter four for both the pessimistic and envelope modelling approaches. The future of climate change is still uncertain; the A1B climate scenario is used here as it offers a balanced view with predicted global warming between the A2 and B1 scenarios. The use of the pessimistic results allows assessment of species protection if species are unable to track climate change through dispersal. The envelope approach provides understanding of the PA protection within a species' suitable climatic areas. To identify these climatically suitable areas for each species, predictions of suitable conditions were made for four time periods (present, 2030, 2055, and 2080). Only climatically suitable areas that are connected to a

species' existing IUCN range over the four time periods are considered, thus removing distant areas and unreachable areas due to climatic constraints. Each species' range consists of a number of 10' grid cells (hereafter cells) across Africa. Each cell is approximately 344km^2 at the equator. For this chapter, calculations of area are based on the number of cells multiplied by 344km^2. The actual cell size varies by latitude, therefore all areas are approximations and are provided as a guide.

Using the methods below, the level of protection currently provided by PAs was analysed, and the suitability of the PAN to protect species to a set of minimum requirements was assessed.

Protected area data

An ARCGIS shape file delimiting all non-maritime protected areas in Africa, excluding Madagascar and Reunion Island, was rasterized to the same scale as the climate data (10' grid cells) using the same methodology described in the project methodology (2.1). The data were provided by the WDPA (United Nations Environment Programme World Conservation Monitoring Centre, 2010). This freely available and up-to-date database contains details of each PA with the global PAN. The ARCGIS shape file is a component part of the WDPA and also provides data about each PA. Only PAs represented by polygons and not points were included (see Pouzols *et al.*, 2014). The WDPA fields used for the selection and filtering of data in this study were: country, IUCN category (see Table 5-1), designation type, status, governance type, marine area, and management authority. These fields, and others, are described in the metadata document provided with the WDPA. There are three levels for these fields that identify whether they are required to be completed before entry into the database. These are 'minimum', 'core', and 'enhanced' signifying respectively that it must be included; that it is a priority for analysis; and data that are considered supplementary but still identified as 'key information' (UNEP-WCMC, 2012). Table 5-2 shows the fields used to subdivide and filter the data used in this study. Using the above fields community led PAs were deemed as such if the governance type was 'indigenous peoples' or 'local communities', or the management authority included the term 'on behalf of villagers', or the English designation was 'communal conservancy'. All of these areas were located in Kenya, Namibia, or Tanzania (KNT).

Many community managed PAs in other African countries are not listed as such in the database. For example Sengwe in Mozambique (Namirembe, *et al*., 2014; Porter-Bolland, *et. al.,* 2012), community forest projects across central Africa, and over 100 projects in

Botswana, amongst many others (Binot *et al.*, 2009). In addition, there are areas that fall under an IUCN or international designation that incorporate local communities that are not listed as such (e.g. Amboseli National Park in Kenya). However, there is a strong community conservation focus in KNT, with Kenya and Tanzania community PAs offering biodiversity protection (Namirembe *et al.*, 2014).

IUCN category	Name	Description
Ia	Strict nature reserve	Purpose: protected areas managed for science Definition: areas possessing some "outstanding or representative ecosystems, geological or physiological features and/or species" The areas are used primarily for research and/or environmental monitoring
Ib	Wilderness area	Purpose: protected areas managed to protect wilderness areas Definition: large areas which are largely unmodified and managed to preserve the natural condition
II	National park	Purpose: protected areas managed for ecosystem protection and recreation Definition: natural areas designated to a) protect ecological integrity of ecosystems for future generations; b) exclude exploitation or occupation harmful to the purpose of the area; and c) provide a "foundation for spiritual, scientific, educational, recreational, and visitor opportunities" provided that they are not environmentally and culturally harmful
III	Natural monument	Purpose: protected areas managed to conserve specific natural features Definition: an area containing one or more features of natural or cultural significance due to unique value, cultural significance, rarity, or aesthetic qualities
IV	Habitat/species management area	Purpose: managed for conservation through management intervention Definition: areas with active management in order to maintain habitats and/or ensure the requirements of specific species
V	Protected landscape/seascape	Purpose: protected areas managed for land/seascape conservation and recreation Definition: areas where the interaction of human and nature have, over time, produced an area of "distinct character with significant aesthetic, ecological and/or cultural values, and often with high biological diversity". These areas are managed to maintain the traditional interactions
VI	Managed resource protected areas	Purpose: protected areas managed for sustainable use of natural ecosystems Definition: areas of largely unmodified natural systems that are managed to enable sustainable use of natural products and services whilst ensuring long-term protection of biodiversity

Table 5-1: IUCN category PA and description – derived from Box 3.3 (Lockwood, 2006).

WDPA field	Field requirement	Field description
Country	Minimum	A three letter code (ISO 3166-1 designation) used to remove the Madagascar (MDG) and Reunion Island (REU) PAs, and select the country specific PAs for the community protected areas
Status	Minimum	The current legal or 'official' standing of the protected area. Either 'Proposed' or 'Designated' are valid entries. Other values were entered; however, all were included in the analysis except for those classified as 'Proposed'
Marine	Minimum	Defines whether the area is a marine PA. Only land based PAs were included.
IUCN category	Core	IUCN management category (Ia, Ib, II, III, IV, V, or VI) where designated for national protected areas (see Table 5-1). Alternatively, international areas may be 'Not Applicable', and 'Not Reported' is also accepted. Other entries, outside the supported options, include Ramsar, Wetland of International Importance, Site of Biological and Ecological Interest (SIBE), and World Heritage Site. This field was used to subdivide IUCN areas from all others for the continent wide analysis
Designation English	Core	The English translation of the type of protected area as legally/officially established or recognized. Values include 'National' for most IUCN category sites, 'International', and many other values including 'Communal Conservancy' which is considered linked to local community conservation
Governance type	Enhanced	This includes the values of 'Indigenous peoples' and 'Local communities' amongst other government, shared, and private governance options. This field is key in identifying community run PAs
Management authority	Enhanced	This is a free field including areas that were run by a group 'on behalf of villagers' and are considered community run PAs

Table 5-2: WDPA fields used to select and categorize PAs from the WDPA.

Country data

To assess the importance and contribution of community managed PAs in these countries, the African dataset was subdivided into countries. An ARCGIS base country shape file (DIVA-GIS, 2012) was rasterized (see 2.1) to obtain the cells that related to each country. These cells were then used as a filter to analyse only these countries. For Tanzania this included Zanzibar and Pemba Island where the Aders' duiker (*Cephalophus adersi*) is present. All other islands around Africa were excluded as no antelopes are present.

Gap analysis

Traditional gap analysis requires four basic steps: 1) Production of a vegetation/land use map; 2) Production of predicted distributions for species; 3) Classification of areas according to their protected status (protected and other land-use categories); and 4) Analysis of the representation of species and vegetation in protected areas. (Rodrigues *et al.*, 2003). Here, I replace vegetation with climate data to predict the distribution of species, incorporating a human footprint filter (see 2.2), before assessing the representation of each species within PAs. This study uses the A1B climate scenario ensemble forecasts produced in chapter four (without the habitat filter applied) to generate the gap analysis results. Overlaying all species ensemble forecasts for the A1B climatic scenario produces a projected species richness map for Africa. For the pessimistic approach this was compared with the present species richness

as defined by the rasterized current IUCN distributions (see chapter three; Figure 5-2). For the envelope approach the 2080 predictions were compared with present species richness based on the climatic suitability for each species, which in turn was based on the bioclimatic model and current climate conditions (Figure 5-3).

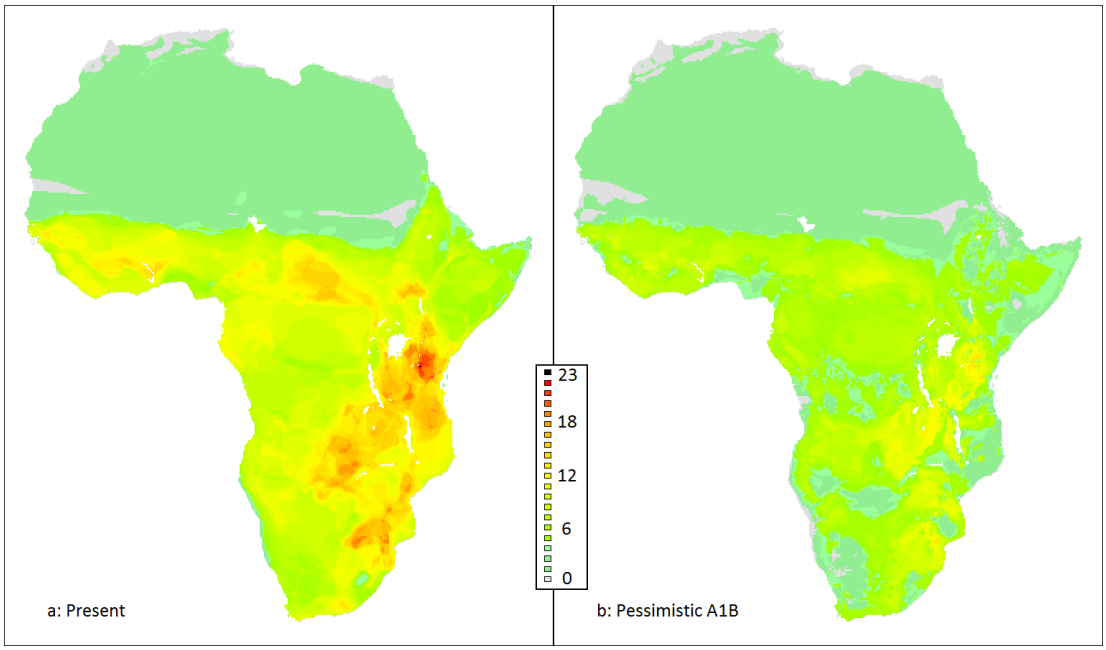

Figure 5-2: Species richness of 73 antelope species in Africa. a: the species richness at present as defined by the IUCN distribution maps. b: the projected species' distribution for 2080 based on ensemble forecasts under the A1B climate projection and pessimistic modelling approach without the habitat filter applied.

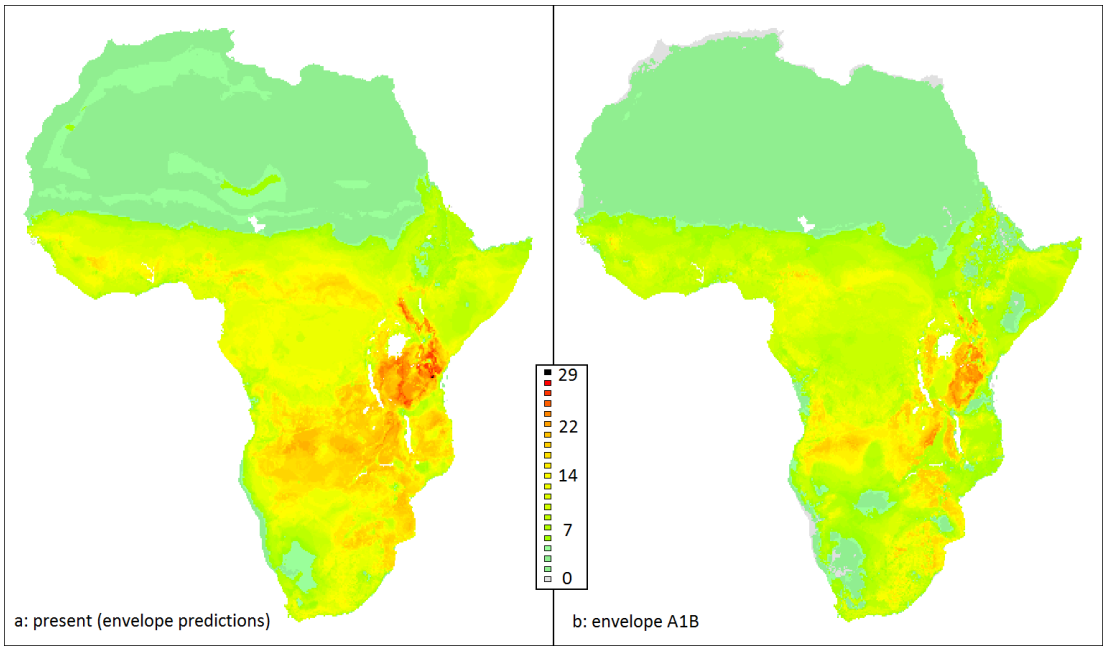

Figure 5-3: Species richness of 73 antelope species in Africa. a: the potential species richness at present based on climatic suitability (envelope approach). b: the projected species distribution for 2080 based on ensemble forecasts under the A1B climate projection and envelope modelling approach without the habitat filter applied.

The results below present the A1B climate scenario for the envelope and pessimistic approaches without the habitat filter applied. The tables show each species' PAN coverage for Africa as well as for Kenya, Tanzania, and Namibia separately, for both approaches. Within each geographic area the PAN was sub-categorized into two or three groups using the WDPA data described above. For Africa, the sub-categories were the IUCN designated PAs which have an IUCN PA category (Ia to VI) assigned (hereafter IUCN PAs), and the non-IUCN designated PAs (hereafter non-IUCN PAs). Where a cell had both IUCN and non-IUCN PAs present, IUCN took precedence and was labelled as such. For the country specific analysis PAs were divided into three distinct categories: IUCN PAs, community PAs, and supplementary PAs. The designation of community PAs is described above and the supplementary PAs include all remaining PAs. Where multiple PA types were present in a cell IUCN PAs take precedence over community PAs, and community PAs over supplementary PAs. This precedence assumes that IUCN PAs, being largely nationally managed, will have longer-term plans and objectives, more stability, and more funding, than the non-IUCN managed community, local government, or privately managed PAs.

Species protection assessment

Separate tables for each of the four regions (Africa, Kenya, Namibia, and Tanzania), and for the two approaches (envelope and pessimistic), present the level of protection provided to each species. The tables are partitioned into four sections:

1. The first partition gives the range of each species within the geographic area's PAN (e.g. 'Range within the African PAN'). This is the absolute number of cells a species' range is projected to occupy in each of the PA categories in 2080. A low value for this statistic characterizes a species that has few areas of protection.
2. The second partition is the percentage of a species' total range protected in that geographic area, subdivided into the categories (e.g. Equation 5-1). A low value for this statistic also highlights a concern for species survival in light of threats outside of protected areas.

$$\%\ IUCN\ coverage\ 2080 = (number\ of\ IUCN\ PA\ cells\ within\ a\ species' range\ in\ 2080)\ /\ (species'\ range\ in\ 2080)$$

Equation 5-1: Example of a percentage of a species' total range within a PA category (here IUCN, but also non-IUCN, community, and supplementary where applicable).

3. The third partition is the change in percentage coverage of each PA type between present and 2080 (Equation 5-2). Negative values suggest the species is less protected in the future than currently.

$$IUCN\ \%\ change\ present\ to\ 2080 = \ (\%\ IUCN\ coverage\ 2080) - (\%\ IUCN\ coverage\ present)$$

Equation 5-2: Example of a change in percentage coverage within a PA category (here IUCN, but also non-IUCN, supplementary and community where applicable) between 2080 and present where the % IUCN coverage present is a similar calculation to Equation 5-1 using the species presence data for the present.

4. The final partition has basic species' data from chapter four. It provides the species' range in 2080 as cells, and the percentage change in range from present to 2080.

Each of the statistics is singularly important, but should be evaluated alongside the others to gain an overall species perspective. The total protection values (coverage by all PAs) are not provided directly, but the values can be added together to provide those statistics.

The tables highlight species that have less than 20,000km^2 (<59 cells where 59 cells represents 20,296km^2) of their range protected by the PAN. This represents the area under which a species may be considered vulnerable by the IUCN under Extent of Occurrence (EOO) (IUCN Standards and Petitions Working Group, 2008). The IUCN methodology defines EOO as being the area with the shortest continuous imaginary boundary encompassing a species (IUCN Standards and Petitions Working Group, 2008). Future ranges may be fragmented and the scale used here is coarser than the IUCN recommendations. Despite suitable climatic conditions, it is unclear whether the cells would be fully populated by a species given variable habitat within that cell. For these reasons the 20,000km^2 limit rather than the 2,000km^2 limit for Area of Occupancy (AOO) is used as a guidance value of where species might be considered vulnerable. In addition, in this study the 20,000km^2 limit represents an area that must be protected rather than the species' true EOO. This is suggestive of a future where species are only safe and viable within protected areas given increased human exploitation threats outside.

Species highlighted in green in the country specific tables under the envelope approach are species which are new, or returning, to the area through dispersal.

Marxan configuration

The Marxan software (Ball *et al.*, 2009) was used to generate the PAN solutions for Africa. To produce these solutions it is necessary to establish how important each cell is to the

protection of species and the wider PAN in general. The concept of irreplaceability of an area, or cell, is defined as a fraction of all valid solutions that require that site (Pressey *et al.*, 1994). This is computationally restrictive and can only be used on small datasets. To counter this, other methods have been produced such as Ferrier *et al*.'s (2000) 'irreplaceability for large datasets', and 'selection frequency', previously called "summed irreplaceability" (Ardron *et al.*, 2010). Selection frequency used by Marxan produces many solutions to the minimum set problem, that being where all species representation targets are met. This is achieved using simulated annealing whereby a solution is produced before being improved repeatedly until all targets are met at the lowest cost.

The configuration of Marxan allows costs to be attributed to each cell, species, and boundary length, to aid in the production of efficient solutions. Boundary length was set as having a high "cost" to the solution (boundary length modifier 10,000). This intentionally results in the clustering of PAs where possible. This setting helps identify larger areas to protect while still meeting the species representation targets. If larger areas are protected species within those PAs have greater opportunity to disperse and behave naturally, and retain a broader gene pool at a lower cost per unit area through economies of scale (Di Minin *et al.*, 2013; Bruner *et al.*, 2004). Larger PAs also reduce the likelihood of species' extinction within those reserves (Brasheres *et al.*, 2001) and are therefore preferred by conservationists (Hannah, 2008; Halpin , 1997; Diamond, 1975). No limit was set for the overall cost of the solution produced as the cost of establishing a PA for each cell was unclear and was set equally low (0.1) except for human transformed areas which were assigned a very high cost (10,000) to preclude their use where possible. The boundary length "cost" is therefore the dominating parameter. Each species was assigned a species penalty factor whereby threatened species are considered more important to the solution than non-threatened (critically endangered 5,000, endangered 4,000, vulnerable 3,000, near threatened 2,000, least concern 1,000. n.b. The silver dik-dik has no threat status and was set as 3,000 due to having a similar size range to other vulnerable species).

In the final Marxan configuration all current IUCN PAs were set as 'locked in' meaning that the IUCN PAs must be present in the final solution, whereas all non-IUCN PAs were set as 'optional'. Setting all existing PAs as optional would produce unrealistic solutions as established PAs might be deemed unnecessary rendering existing infrastructure obsolete.

Run configuration

There is a random element to the production of Marxan solutions and therefore the same solution is not always produced and does not represent the perfect solution described by Pressey (1994). However, by running multiple repetitions a frequency set is produced where solutions overlap. Here 1,000 repetitions were run for two scenarios. The two scenarios, labelled "Low Protection" and "High Protection", employ different strategies for setting the species representation targets, i.e. how many cells are required that provide suitable habitat (see below for representation target settings). Marxan was run both for the pessimistic and envelope approaches. Therefore four complete potential PANs were produced. Moreover, Kenya, Namibia, and Tanzania were extracted from these PANs to specifically assess the importance of community areas in antelope conservation.

Setting species targets

Ideally species specific adequacy data, such as species habitat curves, minimum viable populations, and population density data would be used to produce species protection targets and identify percentages of coverage for each species. However, as in this case those data are not generally available and alternative methods are sought. It is also not possible to apply a blanket percentage for the protection of all species. Large ranged species, for example the dorcas gazelle with a range of over 10,000,000km^2 (29,608 cells; pessimistic approach, A1B climate scenario), assuming a blanket coverage requirement of 20%, would require approximately 2,000,000km^2 (5,922 cells; 6.6% of Africa's land mass) be protected for that one species alone. To counter this, methods for producing more realistic targets have been developed (Ardron *et al.*, 2010). Here I normalize the spatial data using transformations, in this case a square root transformation (see Equation 5-3; Ardron *et al.*, 2010).

Equation 5-3 was used to set the targets for the low and high protection scenarios. The low protection target was set using a theoretical species (y) where 20% of its 1,000 cell range was required to be protected. Using this method a species with a range of 30,000 cells would require 1,095 cells to be protected, approximately 3.7% of its range. For the high protection target, the same method was used with the theoretical species requiring 30% of its 1,000 cell range. This increases the required cells to be protected by 1.5 times for a species of that range. Additionally, proportion requirements can be set. For example, for very small ranged species it is possible to set a proportion requirement of 100% to ensure that those species' entire ranges are protected. Here, a minimum 20,000km^2 (59 cells) is protected for all

species where possible (Table 5-3). As detailed above, the <20,000km^2 range signifies the area for which the IUCN criteria would classify a species as vulnerable based on extent of occurrence.

$$(x_p/y_p) \approx (x_t/y_t)^{0.5}$$

Equation 5-3: Calculation of required cells to be protected where x and y are two species, p is the area protected for a species, and t is the total area for the species. Equation from Ardron et al. (2010).

Species type	Suitable range (Number of cells)	Marxan target representation **Low protection** (Number of suitable cells)	Marxan target representation **High protection** (Number of suitable cells)
Medium to large range species	>59	Equation 5-3 using **20%** protection for a 1,000 cell species	Equation 5-3 using **30%** protection for a 1,000 cell species
Small range species	≤59	Total range protected to ensure at least 20,000km^2 area is protected	Total range protected to ensure at least 20,000km^2 area is protected

Table 5-3: Comparison of Marxan configuration for low and high protection options. The target representation is calculated as either the number of suitable cells or the percentage of suitable cells, whichever is greater.

When individual species assessment is not possible, or the required data is unavailable to produce species specific representation targets, the production of multiple solutions provides options for conservation decision makers (Ardron *et al.,* 2010). The two protection targets used here (i.e. 20% and 30%) are both above the 17% Aichi target as this is considered insufficient to halt biodiversity loss at a global scale (Larsen, *et al*., 2014). Furthermore, these protection targets have been used in previous studies (Klein *et al.*, 2010; Ball *et al.*, 2009; Lourival *et al.*, 2009; Cook & Auster, 2005).

All other statistics and plots were generated using R version 2.15.2 (R Core Team , 2012) and modified versions of BIOMOD's 'level.plot' function (Thuiller *et al.*, 2009). Outliers are defined as deviating from the mean by three times the standard deviation.

Results

Table 5-4 summarizes each geographic zone's PA coverage. The results show that Kenya, Tanzania, and Namibia vary greatly in how the PA types are designated. Of particular note is the high percentage of community PAs, and the low number of nationally governed IUCN areas in Namibia compared to Kenya and Tanzania.

Geographic area	Cells	Total cells covered by PAN (% of total cells)	IUCN PA cells (% of total cells)	Community PA cells (% of total cells)	Non-IUCN (Africa) or supplementary (KNT) PA cells (% of total cells)
Africa	89,380	12,779 (14.3%)	5,997 (6.7%)	Not calculated	6,782 (7.6%)
Kenya	1,654	255 (15.4%)	123 (7.4%)	32 (1.9%)	100 (6.0%)
Namibia	2,600	1,046 (40.2%)	112 (4.3%)	472 (18.2%)	462 (17.8%)
Tanzania	2,590	985 (38.0%)	433 (16.7%)	87 (3.4%)	465 (18.0%)

Table 5-4: Protected area breakdown by geographic area. Percentage values for IUCN, community and other PAs are a proportion of total cells (column 3) for each row.

Figure 5-4a and Figure 5-5a demonstrate the predicted species richness in Africa in 2080 under the envelope and pessimistic approaches respectively. These figures also highlight the location of the existing IUCN PAs (centre maps; b) and non-IUCN PAs (right maps; c).

Below I present the results by geographic region (Africa, Kenya, Tanzania, and Namibia). For each geographic region I firstly present analysis of the protection given by the existing protected area network to each species both at present and in 2080. I then present the Marxan solutions for each region. Each region's results contain separate sections for the two different approaches (envelope followed by pessimistic).

Analysis of Africa's existing protected area network, and future requirements

Envelope approach

One species, the hirola, is forecast to have no climatically suitable areas remaining by 2080 under the envelope approach (Table 5-5). Four species only have suitable habitat outside protected areas, while a further seven species (12 in total including the hirola) are protected in areas under 20,000km^2. At present there are nine species that have less than 20,000km^2 of their climatically suitable range protected. Therefore, three additional species are predicted to be without 20,000km^2 of protection in the future: Addax, Jentink's duiker (*Cephalophus jentinki*), black wildebeest (*Connochaetes gnou*). No existing species, currently under 20,000km^2 of protection, are predicted to increase their level of protection to greater than 20,000km^2 through this approach.

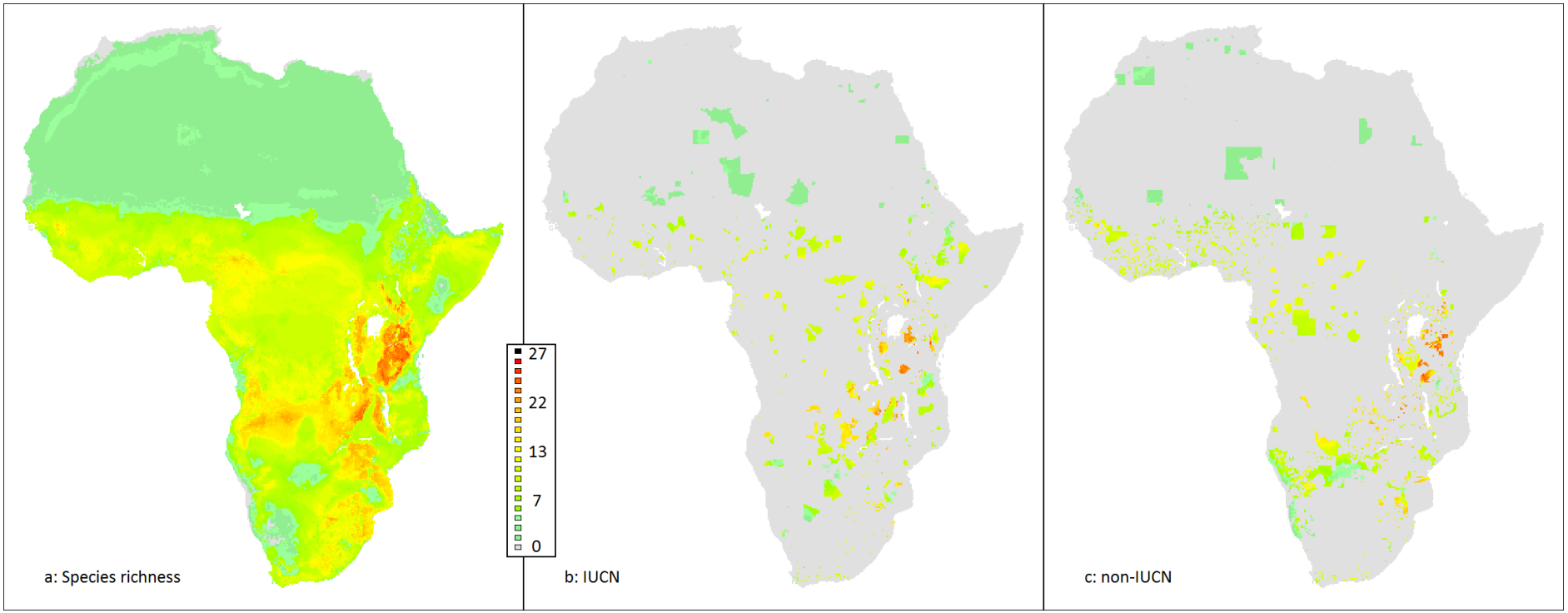

Figure 5-4: Species richness under the envelope approach, A1B climate scenario in 2080. a: presents the species richness across Africa; b: the IUCN designated PAs; c: the remaining non-IUCN PAs.

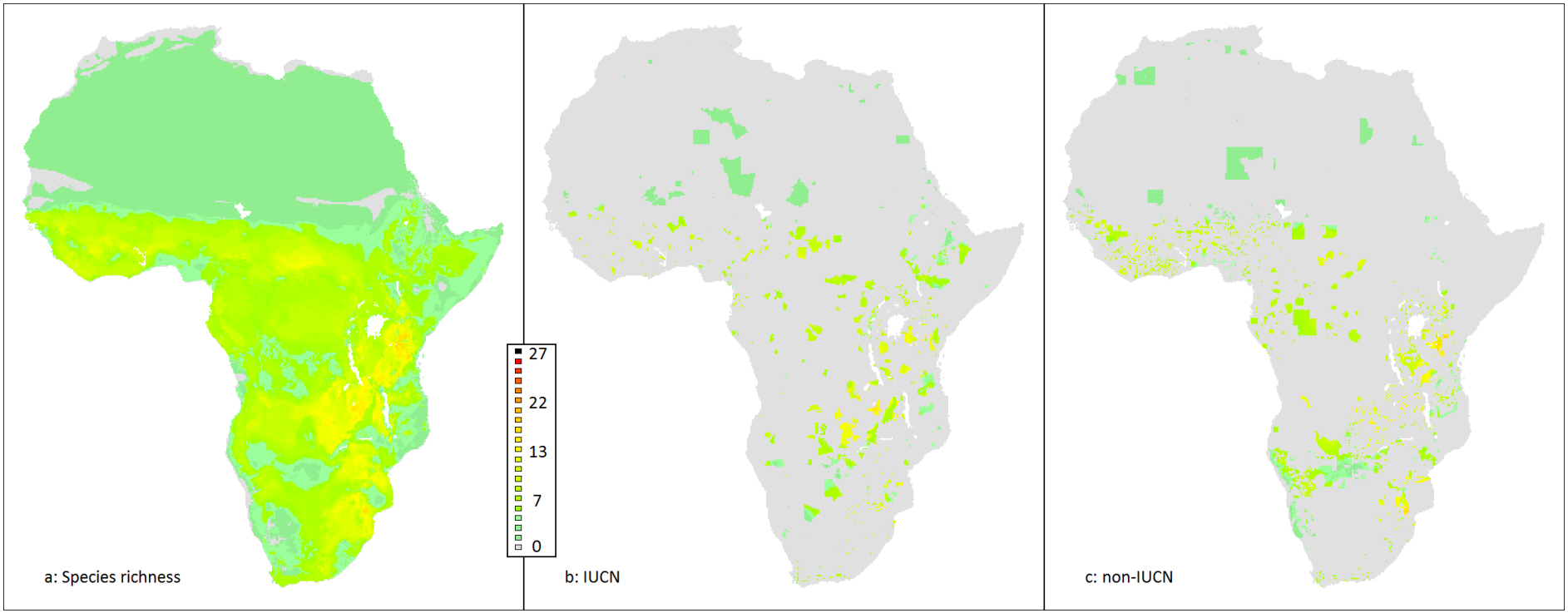

Figure 5-5: Species richness under the pessimistic approach, A1B climate scenario in 2080. a: presents the species richness across Africa; b: the IUCN designated PAs; c: the remaining non-IUCN PAs.

Africa Envelope approach A1B climate scenario	Range within the African PAN		Percentage of range within the PAN		Change in percentage of range within the PAN		Species range	
Species	IUCN PAs in 2080 (cells)	Non-IUCN PAs in 2080 (cells)	IUCN PAs in 2080	Non-IUCN PAs in 2080	Change in IUCN PAs (present to 2080)	Change in non-IUCN PAs (present to 2080)	Range in 2080(cells)	Percentage change (present to 2080)
Hirola	0	0	0	0	-3.33	0	0	-100
Silver dik-dik	0	0	0	0	-1.01	0	68	-90.23
Dibatag	0	0	0	0	-3.61	0	410	-47.1
Speke's gazelle	0	0	0	0	0	0	719	-36.26
Beira	0	0	0	0	-2.84	0	1,043	-44.16
Nile lechwe	2	0	14.29	0	12.85	0	14	-98.74
Aders' duiker	5	0	20	0	20	-1.29	25	-83.87
Abbott's duiker	7	2	19.44	5.56	4.06	-0.21	36	-65.38
Mountain nyala	25	0	92.59	0	15.23	0	27	-49.06
Jentink's duiker	2	25	0.82	10.29	-2.04	-0.97	243	-53.63
Black wildebeest	13	20	1.22	1.88	-0.52	-0.5	1,063	-57.03
Addax	52	6	13.58	1.57	-1.95	1.57	383	-79.7
Blesbok/bontebok	29	40	2.37	3.27	-0.3	0.3	1,223	-47.28
Peters' duiker	51	29	8.11	4.61	2.13	-6.6	629	-90.18
Bates' pygmy antelope	60	31	8.86	4.58	2.61	-5.62	677	-89.05
White-bellied duiker	72	39	7.56	4.09	0.77	-5.75	953	-85.53
Cape grysbok	52	66	3.81	4.84	-0.92	-3.74	1,365	-66.55
Grey rhebok	45	83	3.01	5.56	-0.29	-2.57	1,493	-62.29
Zebra duiker	21	118	2.8	15.71	0.27	2.73	751	-17.38
Dama gazelle	117	26	6.64	1.48	-2.45	-2.82	1,762	-76.26
Soemmerring's gazelle	219	38	6.91	1.2	1.29	0.42	3,168	-14.4
Thomson's gazelle	111	172	14.34	22.22	-0.35	2.82	774	-59.96
Giant eland	69	252	5.03	18.38	-2.64	6.37	1,371	-63.73
Cuvier's gazelle	15	306	0.44	8.89	0.14	1.22	3,444	-31.23
Salt's dik-dik	281	88	7.68	2.41	-0.34	1.39	3,657	-27.41
Royal antelope	72	320	2.96	13.16	-1.05	0.4	2,432	-12.83
Gemsbok	185	295	4.51	7.2	-3.87	-9.84	4,100	-37.75
Springbok	74	408	2.2	12.15	-4.04	-1.57	3,358	-52.88
Black duiker	123	474	3.03	11.66	-1.74	-1.29	4,066	25.69
Gerenuk	440	217	9.56	4.72	-0.29	2.32	4,601	-11.94
Slender-horned gazelle	397	286	5.9	4.25	0.52	-1.66	6,734	-47.99
Beisa oryx	455	254	11.19	6.25	-0.23	1.41	4,066	-22.24
Guenther's dik-dik	503	212	9.16	3.86	-0.42	0.87	5,489	-6.27
Lesser kudu	523	261	10.15	5.07	-1.19	0.02	5,153	-5.14
Southern lechwe	410	377	10.83	9.96	-6.76	-8.19	3,786	-32.38
Black-fronted duiker	358	430	6.09	7.32	0.16	-1.03	5,877	-46.24
Grant's gazelle	527	273	11.19	5.8	-1.27	-1.24	4,710	0.17
Mountain reedbuck	492	321	10.73	7	0.96	-2.49	4,584	-43.78
Harvey's duiker	531	373	17.87	12.55	2.53	0.83	2,971	-46.24
Red-fronted gazelle	512	570	5.86	6.52	-1.15	-0.43	8,739	-6.94
Steenbok	367	756	5.07	10.45	-4.57	-4.55	7,236	-43.36
Impala	442	718	7.08	11.5	-5.97	-4.09	6,242	-56.21
Kirk's dik-dik	492	699	10.88	15.46	0.74	2.52	4,520	-41.45
Weyns' duiker	466	751	6.67	10.76	-0.04	0.23	6,982	-5.8

Africa Envelope approach A1B climate scenario (CONTINUED)	Range within the African PAN		Percentage of range within the PAN		Change in percentage of range within the PAN		Species range	
Species	IUCN PAs in 2080 (cells)	Non-IUCN PAs in 2080 (cells)	IUCN PAs in 2080	Non-IUCN PAs in 2080	Change in IUCN PAs (present to 2080)	Change in non-IUCN PAs (present to 2080)	Range in 2080(cells)	Percentage change (present to 2080)
Suni	519	720	11.41	15.82	-3.29	1.32	4,550	-29.33
Natal red duiker	541	721	11.44	15.25	-2.99	-0.43	4,729	-7.69
Sharpe's grysbok	694	747	9.85	10.6	-1.84	-1.99	7,048	-42.16
Maxwell's duiker	626	886	6	8.49	0.01	-3.04	10,437	52.08
Southern reedbuck	743	784	8.23	8.69	-2.4	-2.06	9,025	-40.08
Sable antelope	742	802	9.66	10.44	-1.89	-1.97	7,681	-42.72
Ogilby's duiker	598	1,059	5.73	10.16	-0.77	-2.56	10,428	41.97
Sitatunga	735	1,070	5.56	8.09	-0.75	0.26	13,219	-10.43
Blue wildebeest	728	1,082	8.23	12.23	-4.2	-1.9	8,844	-28.21
Bay duiker	676	1,169	5.34	9.23	0.03	0	12,661	0.12
Nyala	753	1,096	12.2	17.76	-4.9	-5.34	6,172	44.61
Blue duiker	770	1,122	6.19	9.02	-1.48	0.66	12,436	-33.15
Bongo	668	1,287	4.9	9.43	-0.45	-1.29	13,643	24.11
Klipspringer	793	1,294	7.88	12.86	-3.31	-0.17	10,062	-51.47
Red-flanked duiker	935	1,224	7.37	9.65	-0.54	-0.23	12,683	17.48
Eland	900	1,268	7.55	10.64	-2.97	-1.82	11,913	-40.07
Yellow-backed duiker	931	1,641	5.07	8.94	-0.56	-0.45	18,355	-0.91
Kob	1,146	1,547	7.29	9.84	-0.6	0.02	15,725	35.09
Dorcas gazelle	1,572	1,147	4.79	3.49	-0.07	0.01	32,827	6.01
Topi	1,335	1,510	10.87	12.29	-2.39	-2.04	12,283	-13.02
Greater kudu	1,691	2,003	11.19	13.25	-0.97	0.94	15,118	-24.71
African buffalo	1,943	2,394	7.71	9.49	-1.07	-0.36	25,214	1.16
Roan antelope	2,062	2,304	9.27	10.36	-0.69	-0.28	22,250	11.92
Hartebeest	2,107	2,265	11.19	12.03	-0.38	-0.39	18,830	-5.51
Oribi	2,277	2,412	9.1	9.64	-0.27	0.11	25,030	10.23
Bohor reedbuck	2,473	2,259	9.86	9.01	0.67	-0.61	25,079	28.64
Waterbuck	2,494	2,455	10.41	10.25	0.16	0.28	23,953	-7.88
Common duiker	2,330	2,677	9.91	11.39	0.28	1.07	23,507	-33.81
Bushbuck	2,453	2,582	9.35	9.84	0.18	-0.02	26,235	-18.73

Table 5-5: Protected area network coverage across Africa (envelope modelling approach under the A1B climate scenario) protected by IUCN designated PAs and non-IUCN designations for each species. The table is ordered by the total number of protected cells (not shown) and subsequently by percentage change in species range (present to 2080). Red species have no protection under these predictions. Orange species have fewer than 59 cells (20,000km^2) protected. The number of cells protected by each designation, the percentage of the species' range protected, the change in that percentage, the total species' potential range, and change in that range are shown.

If the Aichi objective of 17% of land cover target were to be protected for each species irrespective of range size (i.e. each species has 17% of its range protected), 33 species would have adequate protection in the future based on the existing PAN, and four species would have this protection under IUCN PAs alone. The average percentage of species ranges protected by the IUCN PAs in 2080 is predicted to be 8.8% with standard deviation (s.d.) of 10.9, whereas the non-IUCN PAs protect 8.2% (s.d.=4.9) (excluding the hirola, n=72). The

IUCN PAs average percentage of range value is strongly influenced by an outlier, the mountain nyala, whose small range is almost completely protected by IUCN PAs. With the mountain nyala removed, the IUCN PAs are predicted to protect, on average, 7.6% (s.d.=4.3) of a species' range, and the non-IUCN PAs to protect 8.3% (s.d.=4.9; n=71) in 2080. These values demonstrate a drop of 0.6% (s.d.=3.5) in the range protected by IUCN PAs, and 0.9% (s.d.=2.5) in the range protected by non-IUCN PAs from present to 2080 (excluding mountain nyala and hirola).

Mountain nyala, Aders' duiker, and Nile lechwe show large increases in the protection provided by IUCN protected areas, however, the absolute range size for these species are relatively small.

Pessimistic approach

In 2080 four species are predicted to have no suitable areas under the pessimistic approach (Table 5-6; Figure 5-5): addax, Aders' duiker, Nile lechwe, and the hirola. In addition, four species only have suitable habitat outside protected areas, while a further eight species have protection in areas under 20,000km^2 (16 total). At present, 11 species have over 20,000km^2 of their existing distribution protected. Therefore the 16 species predicted to have less than 20,000km^2 of protection represents an increase of five. The five additional species are the addax, dama gazelle, Jentink's duiker, Peter's duiker (*Cephalophus callipygus*), and Soemmerring's gazelle (*Nanger soemmerringii*).

The average percentage of species range protected by the IUCN PAs in 2080 is 10.6% (s.d.=14.6), with the non-IUCN PAs protecting 10.8% (s.d.=8.1), excluding the four 'extinct' species (n=69). Six outliers are present: mountain nyala, Thomson's gazelle (*Eudorcas thomsonii*), southern lechwe (*Kobus leche*), dama gazelle, Abbott's duiker (*Cephalophus spadix*), and nyala. With the outliers and extinct species removed (n=63) the IUCN PAs protect, on average, 7.1% (s.d.=4.1) of a species range, and the non-IUCN protect 9.8% (s.d.=5.7). This represents a drop of 1.3% (s.d.=2.3) in the range protected by IUCN PAs, and 0.6% (s.d.=3.1) in the range protected by non-IUCN PAs from present to 2080 (excluding outliers and extinct species).

Africa Pessimistic approach A1B climate scenario	Range within the African PAN		Percentage of range within the PAN		Change in percentage of range within the PAN		Species range	
Species	IUCN PAs in 2080 (cells)	Non-IUCN PAs in 2080 (cells)	IUCN PAs in 2080	Non-IUCN PAs in 2080	Change in IUCN PAs (present to 2080)	Change in non-IUCN PAs (present to 2080)	Range in 2080 (cells)	Percentage change (present to 2080)
Addax	0	0	0	0	-64.65	0	0	-100
Hirola	0	0	0	0	-6.06	0	0	-100
Aders' duiker	0	0	0	0	0	-16.67	0	-100
Nile lechwe	0	0	0	0	-1.85	0	0	-100
Dibatag	0	0	0	0	0	0	5	-97.96
Silver dik-dik	0	0	0	0	0	0	13	-87.25
Beira	0	0	0	0	0	0	78	-32.76
Speke's gazelle	0	0	0	0	0	0	377	-17.51
Abbott's duiker	6	0	66.67	0	8.77	-15.79	9	-52.63
Mountain nyala	14	0	100	0	9.52	0	14	-33.33
Jentink's duiker	0	16	0	10.26	-4.5	-6.14	156	-49.84
Black wildebeest	10	11	1.29	1.42	0.18	-0.36	776	-42.52
Blesbok/bontebok	12	16	1.39	1.85	-0.29	-0.2	866	-34.19
Dama gazelle	17	17	47.22	47.22	-3.97	38.01	36	-95.69
Peters' duiker	13	24	4.29	7.92	-0.07	-11.58	303	-86.09
Soemmerring's gazelle	38	0	11.18	0	-3.44	0	340	-60.23
Bates' pygmy antelope	35	25	10.09	7.2	2.75	-4.57	357	-84.77
Zebra duiker	13	55	4.06	17.19	0.8	-0.65	320	-19.60
Cape grysbok	35	35	8.77	8.77	1.55	0.73	399	-34.48
White-bellied duiker	41	34	8.28	6.87	2.32	-5.22	495	-86.28
Salt's dik-dik	85	0	4	0	-3.14	0	2,123	-34.05
Grey rhebok	40	52	3.87	5.03	-0.77	-0.84	1,033	-44.85
Giant eland	53	62	9.33	10.92	-9.8	0.4	568	-48.50
Thomson's gazelle	61	78	22.43	28.68	1.25	2.26	272	-40.61
Southern lechwe	80	60	30.19	22.64	-10.09	-1.14	265	-53.99
Natal red duiker	45	98	5.31	11.57	-5.49	1.21	847	-68.99
Slender-horned gazelle	17	127	1.67	12.5	0.98	7.99	1,016	-70.82
Harvey's duiker	62	96	11.31	17.52	1.22	2.68	548	-45.80
Nyala	89	112	20.23	25.45	-0.79	2.84	440	-29.94
Royal antelope	27	181	2.68	17.99	0.38	1.3	1,006	-22.62
Cuvier's gazelle	13	219	1.01	17.06	0.24	2.18	1,284	-23.30
Black duiker	44	255	2.59	15.03	-0.94	0.05	1,697	-23.21
Ogilby's duiker	61	242	4.1	16.27	0.29	-0.01	1,487	-8.60
Suni	112	205	7.22	13.21	-4.93	1.38	1,552	-61.91
Mountain reedbuck	177	158	8.88	7.93	-0.74	-1.41	1,993	-38.75
Guenther's dik-dik	336	53	9.62	1.52	-0.28	-0.15	3,493	-12.89
Gemsbok	142	251	4.49	7.94	-4.6	-12.16	3,163	-44.20
Springbok	35	369	1.29	13.57	-5.56	-1.98	2,719	-56.82
Grant's gazelle	228	199	11.45	9.99	-0.23	-1.16	1,991	-12.60
Gerenuk	329	104	9.87	3.12	-0.54	-0.21	3,335	-19.64
Beisa oryx	335	120	16.63	5.96	-0.67	1.23	2,014	-34.35
Maxwell's duiker	108	470	3.38	14.69	0.42	-2.82	3,199	-12.33
Lesser kudu	405	201	10.45	5.18	-1.79	-0.3	3,877	-10.65
Black-fronted duiker	255	355	5.47	7.61	0.44	-1.04	4,663	-50.19

Africa Pessimistic approach A1B climate scenario (CONTINUED)	Range within the African PAN		Percentage of range within the PAN		Change in percentage of range within the PAN		Species range	
Species	IUCN PAs in 2080 (cells)	Non-IUCN PAs in 2080 (cells)	IUCN PAs in 2080	Non-IUCN PAs in 2080	Change in IUCN PAs (present to 2080)	Change in non-IUCN PAs (present to 2080)	Range in 2080 (cells)	Percentage change (present to 2080)
Weyns' duiker	331	315	8.58	8.17	-0.49	-0.32	3,856	-9.55
Red-fronted gazelle	379	441	6.72	7.82	-1.27	0.09	5,639	-17.33
Kirk's dik-dik	222	627	10.44	29.49	0.21	5.96	2,126	-45.90
Sharpe's grysbok	479	375	13.99	10.96	-1.09	-2.74	3,423	-53.07
Impala	345	575	9.05	15.09	-6.55	-1.95	3,811	-63.09
Sable antelope	547	494	13.33	12.04	-2.59	-4.22	4,102	-53.82
Southern reedbuck	543	502	8.28	7.65	-2.17	-2.43	6,561	-53.85
Steenbok	362	726	5.37	10.76	-4.18	-5.3	6,747	-47.03
Topi	438	664	13.85	20.99	-3.98	4.71	3,163	-42.70
Bongo	469	746	7.93	12.61	-0.15	-0.43	5,916	-8.62
Red-flanked duiker	565	766	7.51	10.18	-0.37	0.23	7,524	-12.78
Kob	673	698	8.46	8.78	0.14	0.09	7,952	-9.34
Bay duiker	499	1,023	5.26	10.77	0.13	0.51	9,495	-9.03
Blue wildebeest	624	955	9.99	15.28	-5.13	-1.96	6,249	-34.97
Blue duiker	646	998	5.59	8.64	-2.31	0.58	11,551	-37.25
Sitatunga	690	1,020	7.14	10.55	-2.54	-0.39	9,669	-23.71
Klipspringer	608	1,108	7.88	14.37	-3.91	1.75	7,711	-50.12
Eland	883	1,187	8.02	10.79	-3.22	-1.34	11,005	-46.49
Yellow-backed duiker	866	1,539	5.46	9.7	-1.45	0.01	15,859	-12.06
Dorcas gazelle	1,493	1,070	5.03	3.61	-0.16	-0.25	29,658	-5.78
Bohor reedbuck	1,295	1,434	8.91	9.87	-0.81	0.01	14,528	-15.01
Greater kudu	1,391	1,816	12.74	16.63	-0.41	2.99	10,918	-40.52
Hartebeest	1,728	1,562	12.04	10.88	-0.83	-0.8	14,353	-29.06
Roan antelope	1,723	1,751	12.13	12.33	-0.31	-1.19	14,202	-14.34
Oribi	1,794	1,811	9.48	9.57	-0.45	0.29	18,919	-14.11
African buffalo	1,819	2,177	9.98	11.94	-2.32	-1.27	18,233	-26.21
Waterbuck	2,112	2,033	11.41	10.98	0.56	0.51	18,511	-29.06
Bushbuck	2,348	2,484	9.23	9.76	0.13	-0.16	25,446	-27.90
Common duiker	2,181	2,663	9.53	11.64	0.53	1.2	22,879	-43.45

Table 5-6: Protected area network coverage across Africa (pessimistic modelling approach under the A1B climate scenario) protected by IUCN designated PAs and non-IUCN designations for each species. The table is ordered by the total number of protected cells (not shown) and by percentage change in species range (present to 2080). Red species have no protection under these predictions. Orange species have fewer than 59 cells (20,000km^2) protected. The number of cells protected by each designation, the percentage of the species range protected, the change in that percentage, the total species' potential range, and change in that range are shown.

The outliers described above demonstrate that some species ranges would be largely protected by the existing IUCN PAN. Mountain nyala has its small, reduced range completely protected under existing IUCN PAs, while Abbott's duiker has one third of its range protected. Other species are well protected by a combination of the IUCN and non-IUCN PAs. Dama

gazelle has 94.4% range protection, while lechwe and Thomson's gazelle have over half of their range protected (52.8% and 51.1% respectively).

Considering the results with the outliers included, the pessimistic approach demonstrates an average of 21.4% (s.d.=17.8) of a species' range is protected under the existing PAN, albeit with large variance and 12 outliers. Forty species would have greater than 17% of their range protected by the existing PAN, six of these have 17% range protection under the IUCN PAs alone.

Marxan solutions for Africa

Figure 5-6 and Figure 5-7 present the Marxan solutions for the envelope and pessimistic approach respectively. The solutions for both approaches include high protection (HP) and low protection (LP) scenarios for comparison. In general, the PAN has been optimized to group the PAs where possible, and is based on the existing IUCN PAs. The new areas required are typically seen as expansions of those existing IUCN areas. However, there are also completely new areas selected. Prominent new areas are found in Somalia, in Western Sahara (under the HP envelope scenario only), and Liberia/Sierra Leone (in the HP scenarios). Other notable expansion areas are described in Table 5-7.

The existing IUCN PAN in Africa would supply adequate protection for 14-36 species (Table 5-8). In total 7,032-7,776 cells, or an area of 2,419,008-2,674,994km^2, is required to protect all species to the required levels. This includes a requirement for new PAs covering 296,528-513,248km^2 (862-1,492 cells). Under the LP scenario, the PAN requires an average 13.2% increase in area to protect all species to their targets. Under the HP scenario the average increase in area required is 18.9%. This represents an average of 937.5 or 1,461 cells (322,500km^2 or 502,584km^2) required for the LP and HP scenarios respectively. Non-IUCN PAs make up a relatively small proportion of the Marxan solutions (2.5-3.7% of total cell requirements). The average contribution of non-IUCN PAs to the final PAN solution is slightly higher for the HP scenarios (3.4%) compared with the LP (3.0%).

Area	Country	PA being expanded	Notes
West Africa	Liberia/Sierra Leone	Krahn Bassa National Forest	Protection of multiple species including Jentink's duiker which has little or no IUCN protection depending on modelling approach
Central Africa	Cameroon	Douala Edéa Wildlife Reserve	Protection of nine duiker species (bay duiker [*Cephalophus dorsalis*], black duiker [*C. niger*], black-fronted duiker [*C. nigrifrons*], Ogiby's duiker [*C. ogilbyi*], Peter's duiker [*C. callipygus*], white-bellied duiker *[C. leucogaster],* Weyns' duiker [*C. weynsi*], Yellow-backed duiker [*C. silvicultor*] and blue duiker [*Philantomba monticola*]) and up to a further five species (bongo, sitatunga, *Bate's* pygmy antelope [*Neotragus batesi*], kob, African buffalo)
	Central African Republic	Bamingui-Bangoran NP; Manovo-Gounda St.Floris; Yata-Ngaya Faunal Reserve	Linking of areas into South Sudan and Sudan.
East Africa	Ethiopia	Eastern Hararghe; Bale Mountain NP; Abijatta-Shalla Lakes; Akobo;	Linking of multiple small IUCN PAs across Ethiopia
	Kenya/Tanzania	Serengeti; Ngorongoro; Amboseli; Tsavo; Selous	See country specific sections below
	Somalia	New PAs	New PAs for species without any existing protection (beira [*Dorcatragus megalotis*], *Speke's gazelle* [*Gazella spekei*], dibatag, and silver dik-dik
Southern Africa	Zambia	Kansonso-Busanga	Linking of multiple PAs centered in Zambia
	Botswana/South Africa	Kgalagadi Transfrontier Park	General expansion of existing area
	South Africa	Cape Town through to Port Elizabeth	Multiple expansions and interconnections

Table 5-7: General areas of large scale PAN expansion suggested by Marxan under all scenarios

In general the differences between the HP and LP solutions for each approach are subtle. The use of a high value boundary length modifier in the Marxan configuration results in larger areas being considered more cost efficient than new small independent areas. The differences are therefore represented as expansions of PAs rather than being significantly different PA locations.

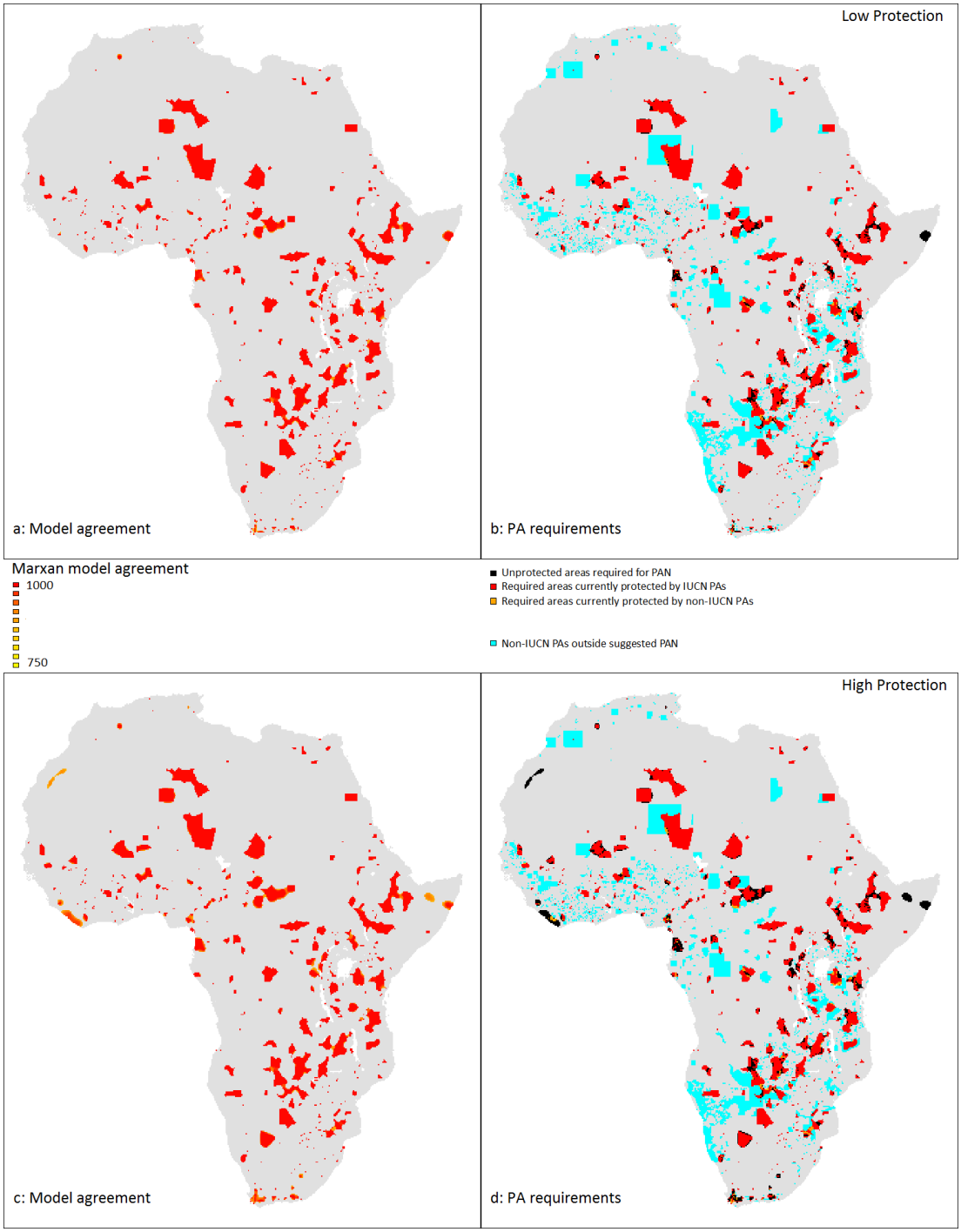

Figure 5-6: Marxan results producing a PAN protecting all species for the envelope A1B scenario. Both low (top panel) and high (bottom panel) protection options are provided (see methods). a and c: The number of Marxan models agreeing (750 - 1000) from a 1000 repetition analysis. b and d: The current protected nature of the areas required for the PAN in a & c. All IUCN areas are required in the future PAN suggesting a baseline PAN (red). Orange areas are currently protected by other organizations or groups. Black areas are required for the PAN to complete coverage.

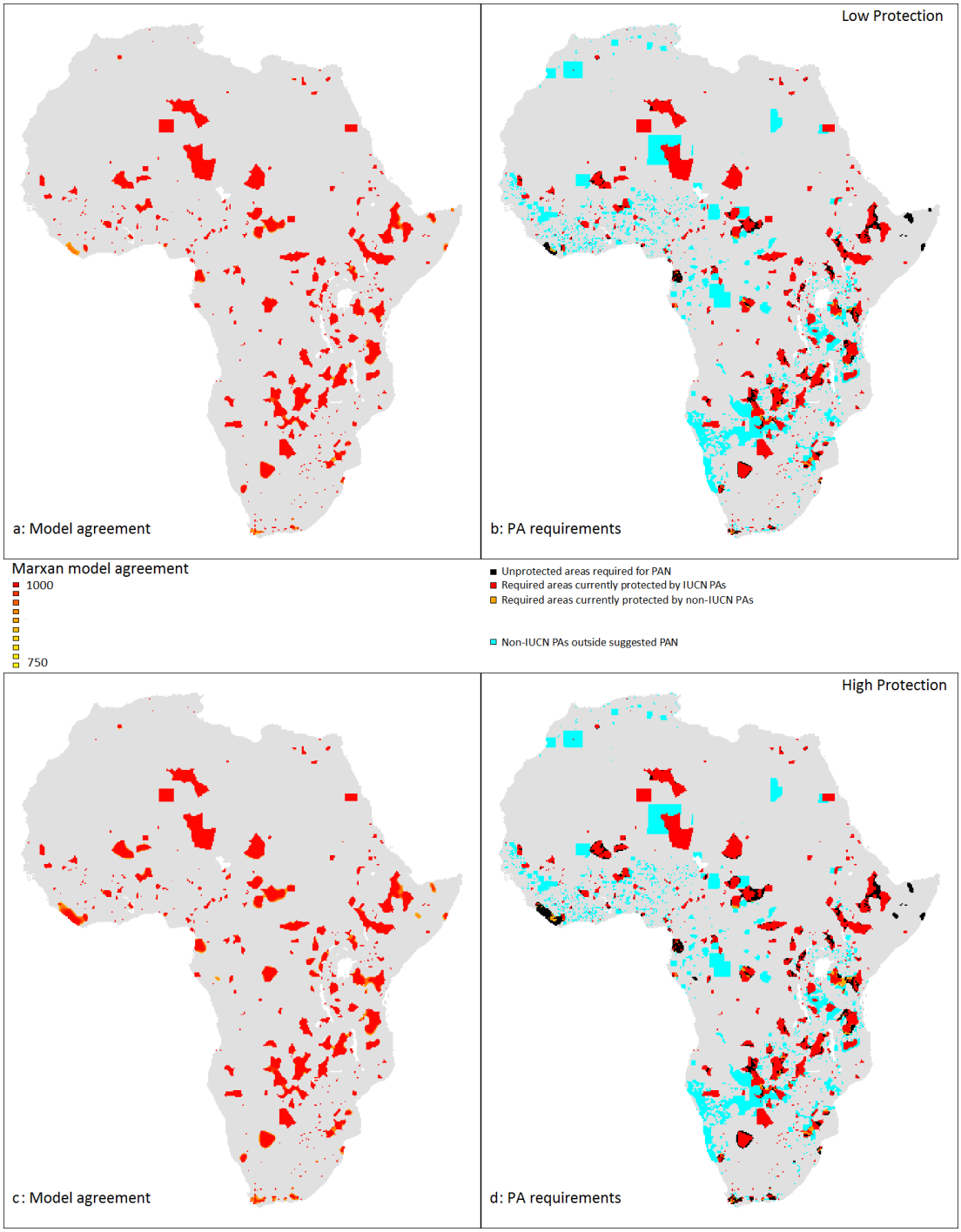

Figure 5-7: Marxan results producing a PAN protecting all species for the pessimistic A1B scenario. Both low (top panel) and high (bottom panel) protection options are provided (see methods). a and c: The number of Marxan models agreeing (750 - 1000) from a 1000 repetition analysis. b and d: The current protected nature of the areas required for the PAN in a & c. All IUCN areas are required in the future PAN suggesting a baseline PAN (red). Orange areas are currently protected by other organizations or groups. Black areas are required for the PAN to complete coverage.

		Number of species adequately protected by current IUCN PAs according to Marxan specifications	Required cells already protected			Additional cells required to provide complete coverage for all species	Total cells required to provide complete coverage for all species	Non-IUCN PA cells not required for antelope PAN coverage
Country	**Scenario**	**Species**	**IUCN**	**Community**	**Other**	**Unprotected**	**Required**	**Other**
Africa	Pessimistic Low Protection	29	5997	Not Applicable	199	1,013	7,209	6,583
Africa	Envelope Low Protection	36			173	862	7,032	6,609
Africa	Pessimistic High Protection	14			287	1,492	7,776	6,495
Africa	Envelope High Protection	14			233	1,430	7,660	6,549
Kenya	Pessimistic Low Protection	Not Applicable	123	1	7	27	158	124
Kenya	Envelope Low Protection			1	7	36	167	124
Kenya	Pessimistic High Protection			1	8	27	159	123
Kenya	Envelope High Protection			1	7	39	170	124
Namibia	Pessimistic Low Protection	Not Applicable	112	7	7	22	148	920
Namibia	Envelope Low Protection			7	5	9	133	922
Namibia	Pessimistic High Protection			7	10	31	160	917
Namibia	Envelope High Protection			7	5	17	141	922
Tanzania	Pessimistic Low Protection	Not Applicable	433	14	25	68	540	513
Tanzania	Envelope Low Protection			5	22	37	497	525
Tanzania	Pessimistic High Protection			22	59	104	618	478
Tanzania	Envelope High Protection			8	38	50	529	506

Table 5-8: The number of cells (each cell ~344km²) that are required to provide protection for all antelope species based on Marxan PAN solutions, including a breakdown of the number of areas already protected by PA type. Three countries are considered separately to assess the importance of community PAs where there have been identified as such. The number of species that will be protected to the target requirement by existing IUCN PAs is recorded for Africa only as the individual countries are a subset of the African PAN and values would not be representative.

Analysis of the contribution of community conservation to the PAN by country

Below, for Kenya, Tanzania, and Namibia, I present the protection provided by the existing PAN for each species. I also present the Marxan PAN solutions for each country, and identify the contribution of community PAs compared with IUCN PAs and supplementary PAs.

Kenya

15.4% of Kenya's cells (255 of 1,654; 87,720 of 568,976km^2) are either completely or partly covered by PAs (Table 5-4). Figure 5-8 and Figure 5-9 highlight large areas of high diversity with no protection in the south-west.

Kenya - envelope approach

Under the envelope approach Kenya provides conditions suitable for over half (39 of 73) of Africa's antelope species in 2080 (Table 5-9). As in the African analysis, the hirola is predicted to have no suitable areas and is lost from Kenya. Seven species, not currently present in Kenya, will have suitable areas (designated "New"). Two of these, the kob which was previously present in Kenya (IUCN SSC Antelope Specialist Group, 2008c), and red-flanked duiker (*Cephalophus rufilatus*), are unprotected. In total 15 species have less than 20,000km^2 of protection within the Kenyan PAN. This represents an increase of six species that will have less than 20,000km^2 of protection compared with the present. Four of these six species are new to Kenya (Kob, red-flanked duiker, bay duiker [*Cephalophus dorsalis*], and Sharpe's grysbok [*Raphicerus sharpei*]) while two are already present (Thomson's gazelle, and Steenbok [*Raphicerus campestris*]).

Kenya - pessimistic approach

Of the 35 species currently residing in Kenya, four species will have no suitable areas if they are constrained to their current areas *as per* the pessimistic approach methodology (Table 5-10). The four are Aders' duiker, sable (*Hippotragus niger*), bongo (*Tragelaphus eurycerus*), in addition to the hirola from the envelope approach. A further two have no PA provision, and 12 more (total 18) have less than 20,000km^2 of protection. The 18 species with less than 20,000km^2 of protection represent an increase of three species from present, those being the hartebeest (*Alcelaphus buselaphus*), suni (*Nesotragus moschatus*), and steenbok.

The silver dik-dik is reduced to a single cell in Kenya, while the blue wildebeest has a range reduction of 94.2%. Other species of concern are the topi (*Damaliscus lunatus*), yellow-backed duiker (*Cephalophus silvicultor*), and the Weyns' duiker (*Cephalophus weynsi*) which have range sizes under five cells (<1,720km).

Kenya Envelope approach A1B climate scenario	Range within the Kenyan PAN			Percentage of range within the Kenyan PAN			Change in percentage of range within the Kenyan PAN			Species range	
Species	IUCN PAs in 2080 (cells)	Community PAs in 2080 (cells)	Supplementary PAs in 2080 (cells)	IUCN PAs in 2080	Community PAs in 2080	Supplementary PAs in 2080	Change in IUCN PAs (present to 2080)	Change in community PAs (present to 2080)	Change in supplementary PAs (present to 2080)	Range in 2080(cells)	Percentage change (present to 2080)
Hirola	0	0	0	0	0	0	-3.39	0	0	0	-100
Kob	0	0	0	0	0	0	0	0	0	11	New
Red-flanked duiker	0	0	0	0	0	0	0	0	0	15	New
Weyns' duiker	0	0	2	0	0	100	0	0	0	2	0
Blue wildebeest	0	0	2	0	0	10	-6.86	-1.96	-1.76	20	-80.39
Aders' duiker	5	0	0	20	0	0	20	0	-3.39	25	-57.63
Bay duiker	1	1	4	1.54	1.54	6.15	0	0	0	65	New
Yellow-backed duiker	2	3	5	2.74	4.11	6.85	0.47	4.11	2.3	73	65.91
Sitatunga	2	3	5	2.41	3.61	6.02	2.41	3.61	1.19	83	33.87
Oribi	5	2	4	8.62	3.45	6.9	1.48	-0.84	-0.25	58	-17.14
Steenbok	4	2	12	4.6	2.3	13.79	-1.97	-3.88	-1.26	87	-66.41
Black-fronted duiker	6	4	8	6.12	4.08	8.16	4.56	2.52	1.91	98	53.12
Blue duiker	9	4	21	4.35	1.93	10.14	-0.25	-0.37	2.67	207	18.97
Thomson's gazelle	9	4	27	5.45	2.42	16.36	-5.35	-2.1	3.8	165	-58.54
Sharpe's grysbok	11	12	34	4.14	4.51	12.78	0	0	0	266	New
Hartebeest	48	2	11	30.38	1.27	6.96	0.38	-1.23	-2.2	158	31.67
Sable antelope	18	14	36	6.21	4.83	12.41	-5.72	0.24	-0.43	290	-11.31
Southern reedbuck	14	13	41	4.49	4.17	13.14	0	0	0	312	New
Soemmerring's gazelle	35	15	23	4.27	1.83	2.8	0	0	0	820	New
Eland	19	14	41	6.05	4.46	13.06	-7.95	0.22	2.56	314	-42.17
Impala	21	16	41	6.73	5.13	13.14	-7.82	1.28	3.27	312	-47.83
Natal red duiker	32	14	39	9.41	4.12	11.47	0	0	0	340	New
Klipspringer	25	14	53	6.78	3.79	14.36	-2.58	0.18	4.2	369	-50.67
Topi	41	15	40	12.06	4.41	11.76	-8.12	0.5	3.63	340	2.41
Mountain reedbuck	51	5	45	8.57	0.84	7.56	-2.96	-1.86	-0.66	595	-26.99
Harvey's duiker	41	11	52	10.35	2.78	13.13	-3.01	-0.12	2.99	396	-36.23
Suni	38	19	51	8.9	4.45	11.94	-7.49	1.13	3.47	427	-21.36
Greater kudu	42	21	52	9.52	4.76	11.79	-0.68	1.72	6	441	-56.72
Kirk's dik-dik	52	12	52	10.57	2.44	10.57	2.08	0.19	5.05	492	-64.3
Salt's dik-dik	68	17	44	7.02	1.76	4.55	-0.63	0.42	1.34	968	-13.8
Common duiker	43	21	73	7.57	3.7	12.85	-5.66	0.33	2.86	568	-29.09
Bohor reedbuck	80	17	42	14.6	3.1	7.66	-3.75	0.18	-0.05	548	45.74
African buffalo	90	10	49	9.64	1.07	5.25	-3.55	-0.46	-1.96	934	43.25
Beisa oryx	80	24	53	7.91	2.37	5.24	-0.12	0.67	1.15	1,011	-21.87
Waterbuck	92	20	50	14.38	3.12	7.81	0.05	0.04	-0.35	640	-1.39
Bushbuck	78	20	65	13.24	3.4	11.04	-0.2	0.3	0.53	589	-8.96
Gerenuk	95	20	52	7.96	1.68	4.36	-0.28	0.03	0.12	1,194	-6.35
Grant's gazelle	96	19	55	7.55	1.49	4.33	-0.24	-0.29	-0.2	1,271	-5.64
Lesser kudu	99	20	57	7.73	1.56	4.45	-0.22	-0.18	0.06	1,280	-3.03
Guenther's dik-dik	105	24	58	8.02	1.83	4.43	-0.11	0.21	0.17	1,310	1.31

Table 5-9: Protected area network coverage across Kenya (envelope modelling approach under the A1B climate scenario) protected by IUCN designated PAs, community PAs, and supplementary PAs for each species. The table is ordered by the total number of protected cells (not shown) and by percentage change in species range (present to 2080). Red species have no protection under these predictions. Orange species have fewer than 59 cells protected (20,000km^2). Species which have "New" in the final column are new to the area. Percentage and change in percentage of the species' range is presented for each PA type.

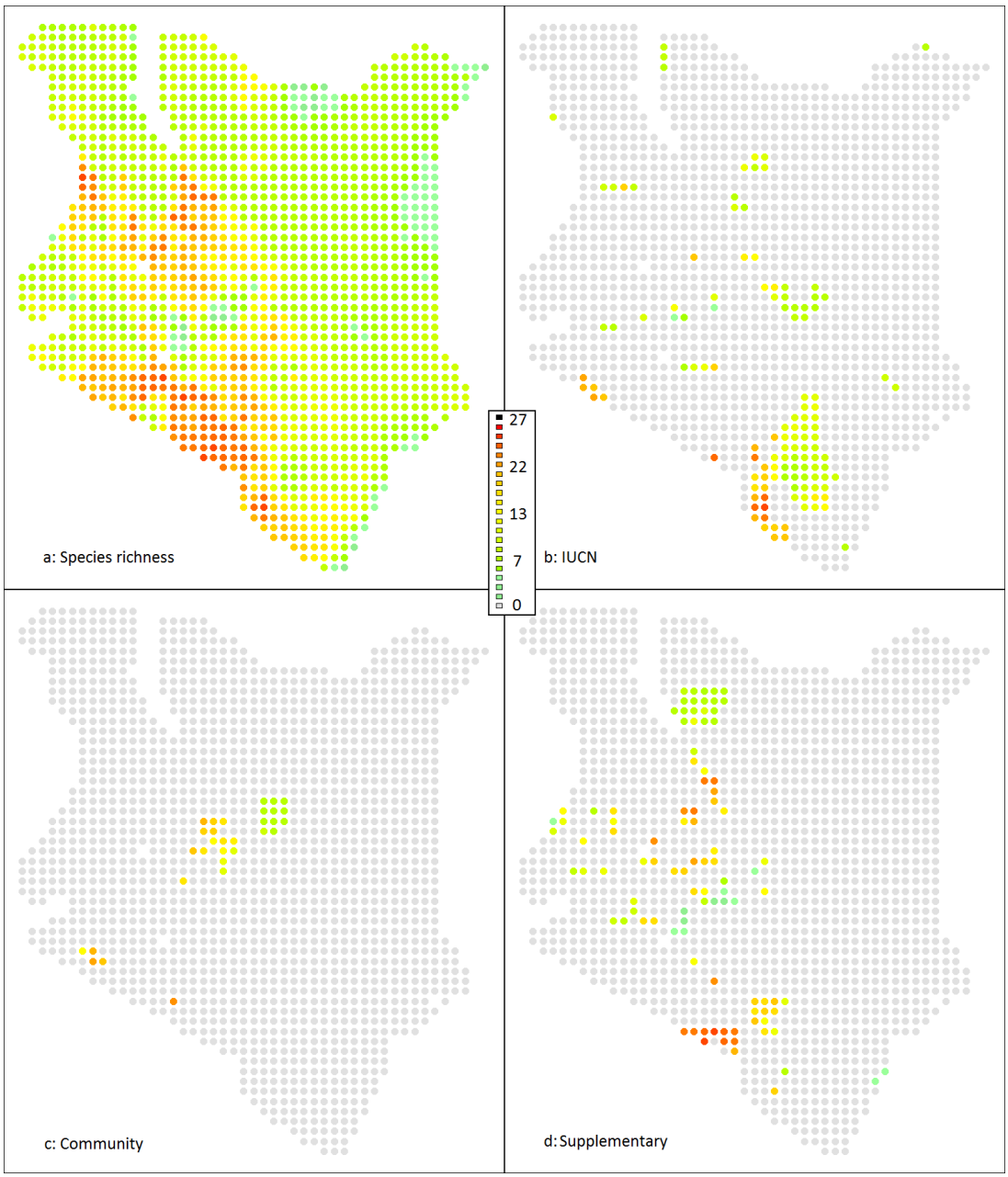

Figure 5-8: Species richness in Kenya under the envelope approach, A1B climate scenario. a: presents the countrywide species richness; b: IUCN designated PAs; c: Community designated PAs; d: the remaining supplementary PAs. Each point represents a grid cell approximately 344km² at the equator.

Kenya Pessimistic approach A1B climate scenario	Range within the Kenyan PAN			Percentage of range within the Kenyan PAN			Change in percentage of range within the Kenyan PAN			Species range	
Species	IUCN PAs in 2080 (cells)	Community PAs in 2080 (cells)	Supplementary PAs in 2080 (cells)	IUCN PAs in 2080	Community PAs in 2080	Supplementary PAs in 2080	Change in IUCN PAs (present to 2080)	Change in community PAs (present to 2080)	Change in supplementary PAs (present to 2080)	Range in 2080(cells)	Percentage change (present to 2080)
Hirola	0	0	0	0	0	0	-6.06	0	0	0	-100
Aders' duiker	0	0	0	0	0	0	0	0	-33.33	0	-100
Sable antelope	0	0	0	0	0	0	-11.11	0	0	0	-100
Bongo	0	0	0	0	0	0	-27.78	0	-61.11	0	-100
Salt's dik-dik	0	0	0	0	0	0	0	0	0	1	-66.67
Blue wildebeest	0	0	0	0	0	0	-17.99	-4.32	-15.83	8	-94.24
Topi	1	0	0	100	0	0	92.8	-1.6	0	1	-99.2
Yellow-backed duiker	1	0	0	33.33	0	0	19.05	0	-21.43	3	-78.57
Sitatunga	0	0	1	0	0	2.22	0	0	-5.78	45	-10
Weyns' duiker	0	0	2	0	0	100	-7.69	0	57.69	2	-92.31
Black-fronted duiker	0	0	2	0	0	40	-17.14	0	2.86	5	-85.71
Oribi	5	2	4	8.77	3.51	7.02	5.6	1.92	1.73	57	-69.84
Harvey's duiker	7	1	5	17.5	2.5	12.5	6.28	1.48	-1.79	40	-59.18
Steenbok	4	2	9	5.33	2.67	12	-8.8	-0.24	0.57	75	-84.41
Blue duiker	7	4	8	5.51	3.15	6.3	0.38	0.59	-0.11	127	-18.59
Thomson's gazelle	5	4	13	4.59	3.67	11.93	-7.84	-2.54	0.13	109	-32.3
Hartebeest	35	2	11	30.97	1.77	9.73	15.61	-0.46	-1.4	113	-74.83
Suni	26	3	26	12.94	1.49	12.94	-6.87	0.5	2.04	201	-50.25
Eland	18	12	31	7.5	5	12.92	-7.24	2	4.91	240	-65.67
Mountain reedbuck	18	5	40	5.84	1.62	12.99	0.54	-1.67	2.39	308	-55.87
Impala	20	16	41	6.76	5.41	13.85	-6.44	2.82	3.62	296	-63.5
Guenther's dik-dik	29	20	31	3.16	2.18	3.38	0.1	-0.27	-0.71	917	-6.33
Greater kudu	31	17	42	10.13	5.56	13.73	2.96	3.42	4.79	306	-61.51
Klipspringer	24	14	53	6.56	3.83	14.48	-0.28	0.98	3.66	366	-58.31
Bohor reedbuck	64	11	28	19.45	3.34	8.51	6.58	0.61	-1.24	329	-57.22
Kirk's dik-dik	51	12	49	11.51	2.71	11.06	1.11	-0.18	4.73	443	-59.95
Common duiker	43	21	73	7.69	3.76	13.06	-3.44	0.73	5.05	559	-45.41
African buffalo	86	10	47	13.27	1.54	7.25	4.05	-0.88	-0.31	648	-51.02
Beisa oryx	78	21	48	9.18	2.47	5.65	-0.35	0.34	0.47	850	-21.37
Gerenuk	87	20	42	10.14	2.33	4.9	0.07	-0.27	-0.3	858	-10.9
Bushbuck	67	20	64	11.99	3.58	11.45	2.58	0.54	2.93	559	-45.25
Grant's gazelle	84	19	49	7.39	1.67	4.31	-0.25	-0.75	-0.91	1,136	-14
Waterbuck	86	20	50	15.38	3.58	8.94	4.99	0.66	1.56	559	-49.04
Lesser kudu	97	19	51	8.18	1.6	4.3	-0.03	-0.45	-0.36	1,186	-6.39

Table 5-10: Protected area network coverage across Kenya (pessimistic modelling approach under the A1B climate scenario) protected by IUCN designated PAs, community PAs, and supplementary PAs designations for each species. The table is ordered by the total number of protected cells (not shown) and by percentage change in species range (present to 2080). Red species have no protection under these predictions. Orange species have fewer than 59 cells protected (20,000km^2).

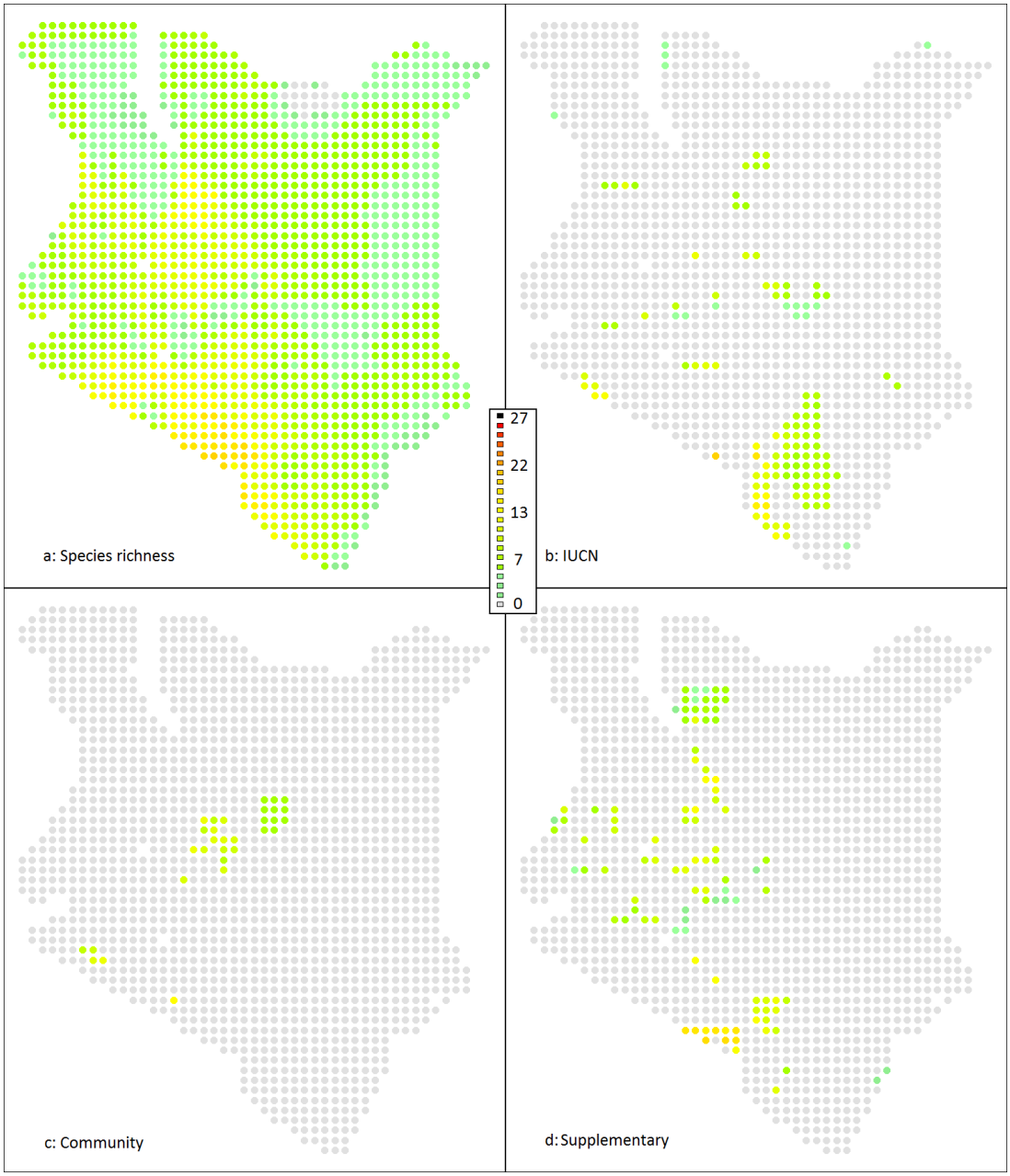

Figure 5-9: Species richness in Kenya under the pessimistic approach, A1B climate scenario. a: presents the countrywide species richness; b: IUCN designated PAs; c: Community designated PAs; d: the remaining supplementary PAs. Each point represents a grid cell approximately 344km^2 at the equator.

Kenya – Marxan solution

As part of the Africa PAN solutions, Kenya provides a total of 54,352-58,480km^2 of protection (158-170 cells; Table 5-8) representing 9.6-10.3% of the country's area (Figure 5-10 and Figure 5-11). The solutions include only one of the 32 community cells on the border with Tanzania. Depending on the scenario and approach, between 7-8% of existing supplementary PAs contribute to the PAN (Table 5-8). In addition to the existing IUCN, community and supplementary PAs, a further 9,288-13,416km^2 (27-39 cells) of new protection is required representing a 10.6-15.3% increase in the current Kenyan IUCN PAN.

The new areas required in all scenarios include an area to the south of the country near Tsavo East National Park (NP) and Tsavo West NP that produces a larger contiguous area. Tsavo is also connected to Amboseli NP on the Tanzanian border and would produce a large transfrontier park between these countries. Under the pessimistic HP scenario, this network of PAs would extend all the way to the Serengeti in Northern Tanzania (see below). To the north of the country, on the border with Ethiopia, to the east of Lake Turkana, Sibiloi NP is expanded to the north and east. This joins Murle NP and Chelbi Wildlife Sanctuary across the Ethiopian border. To the west of the country, under the envelope HP scenario, an area bordering Uganda is important and extends the Amudat NP in Uganda. Finally there are expansions of the existing IUCN PAs in the centre of the country.

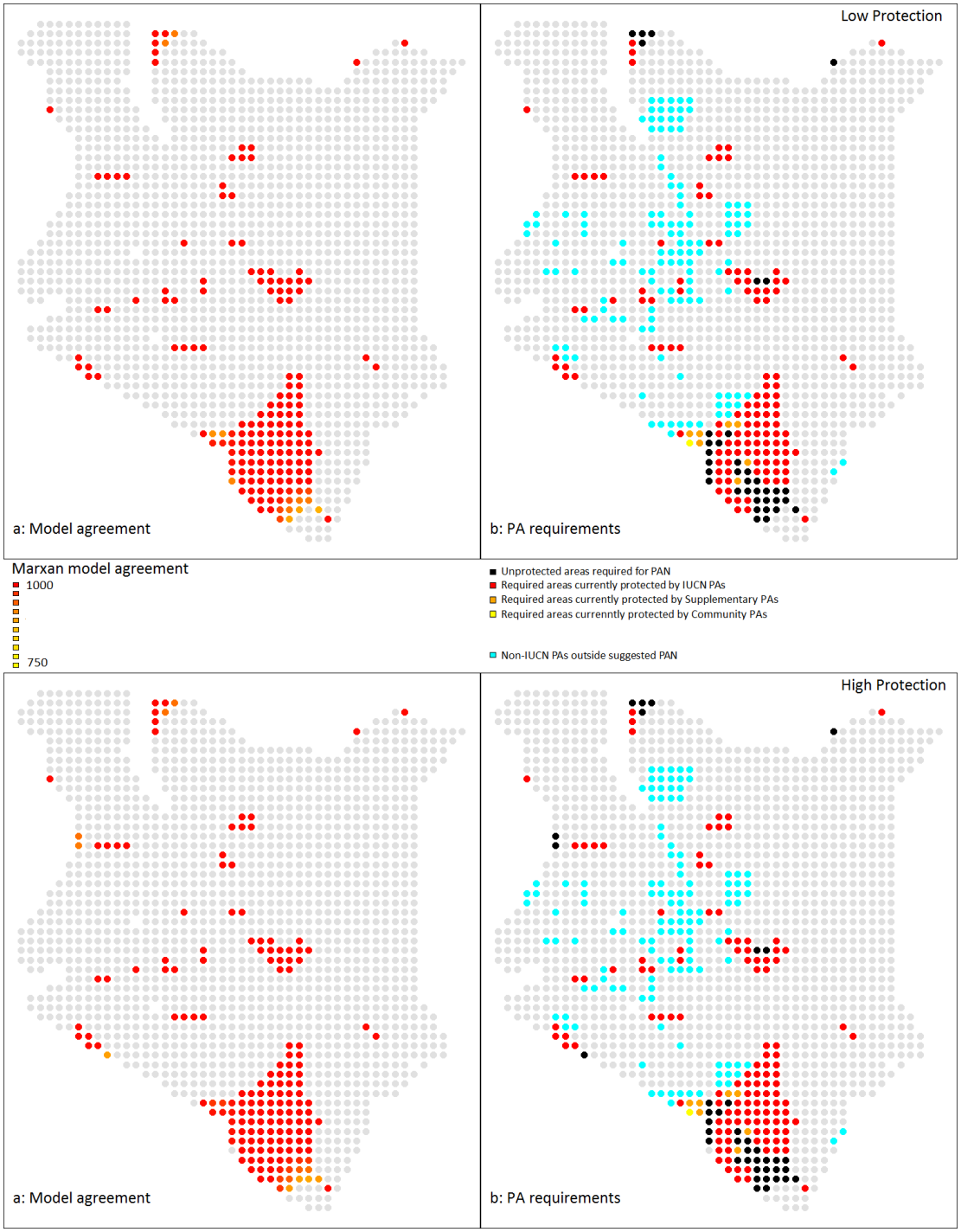

Figure 5-10: The envelope approaches Kenyan contribution to the Marxan produced PAN comparing the low(top) and high (bottom) protection options (see methods). a (left): The number of Marxan models agreeing (750 - 1000) from a 1000 repetition analysis. b (right): The current protected nature of the areas required for the PAN in (a). All IUCN areas are required in the future PAN suggesting a baseline PAN (red). Orange areas are currently protected by other organizations or groups. Black areas are required for the PAN to complete coverage. Each point represents a grid cell approximately 344km² at the equator.

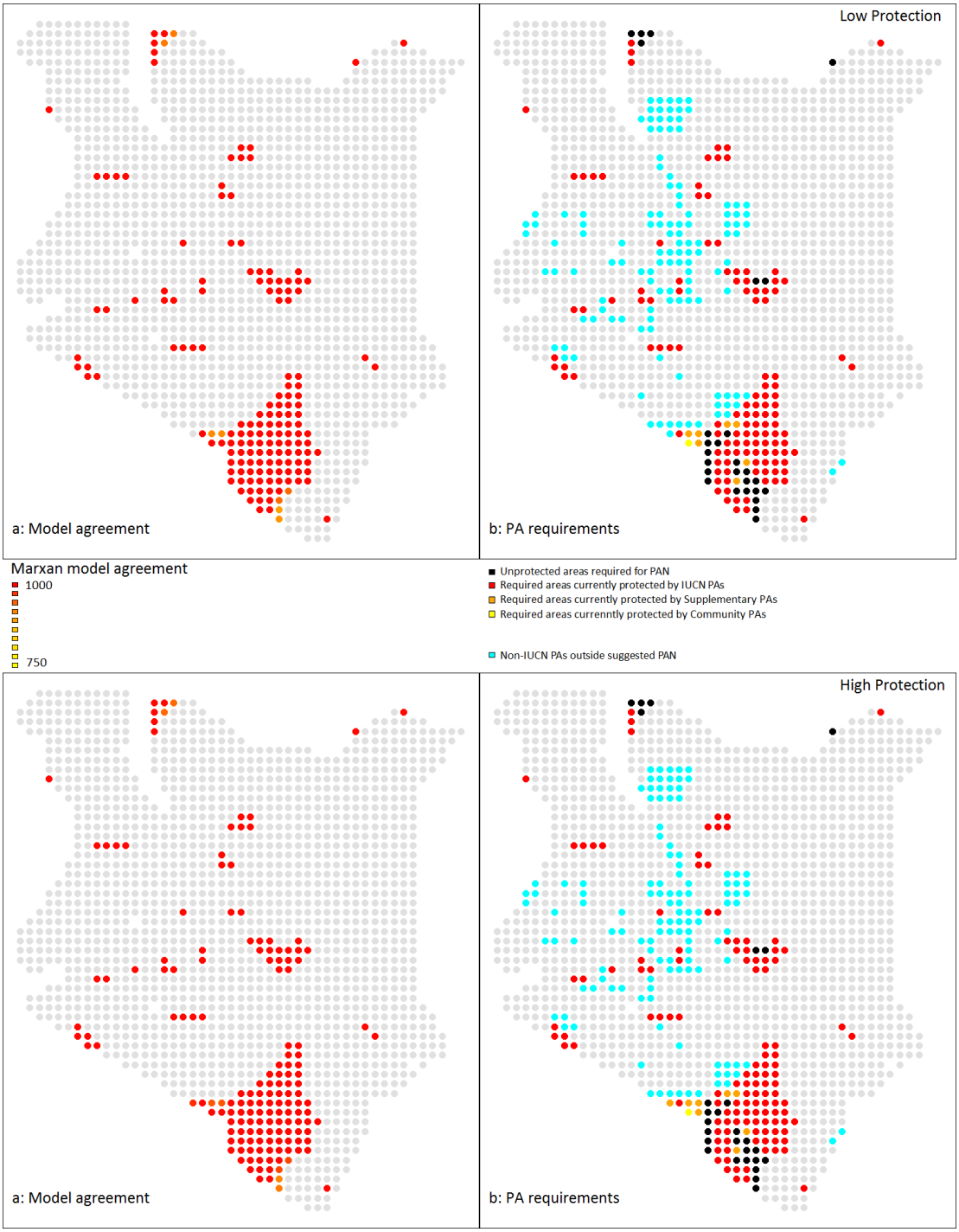

Figure 5-11: The pessimistic approaches Kenyan contribution to the Marxan produced PAN comparing the low(top) and high (bottom) protection options (see methods). a (left): The number of Marxan models agreeing (750 - 1000) from a 1000 repetition analysis. b (right): The current protected nature of the areas required for the PAN in (a). All IUCN areas are required in the future PAN suggesting a baseline PAN (red). Orange areas are currently protected by other organizations or groups. Black areas are required for the PAN to complete coverage. Each point represents a grid cell approximately 344km^2 at the equator.

Tanzania

38.0% of Tanzania's cells (985 of 2,590 cells; 338,840 of 890,960km^2) are either completely or partly covered by PAs (Table 5-4).

Tanzania - envelope approach

For the 2080 time period Tanzania provides suitable climatic conditions for 37 of Africa's antelope species (Table 5-11). Aders' duiker is predicted to have no suitable area remaining. Five species have the possibility for dispersal into suitable areas in Tanzania for the 2080 time period. These five are the yellow-backed duiker, Salt's dik-dik (*Madoqua* saltiana), bay duiker, black-front duiker (*Cephalophus nigrifrons*), and Günther's dik-dik (*Madoqua guentheri*). Weyns' duiker retains a single cell of suitable conditions which is not protected. In total eight species have less than 20,000km^2 protection in Tanzania. These eight represent an increase of five compared to present and include three of the new species (yellow-backed duiker, Salt's dik-dik, and bay duiker), and two existing species (blue wildebeest, and steenbok) with low protection. Furthermore, steenbok has a contraction in its Tanzanian range of over 90%.

Tanzania has the highest present and predicted antelope diversity in Africa. Two cells have the highest species richness: 26 species (see Figure 5-12). However, high diversity areas (i.e. where species richness in a cell is greater than 23 based on 10% of 26 species) contained no threatened species based on current IUCN ratings.

Tanzania - pessimistic approach

32 species are present in Tanzania in the future under the pessimistic approach, and the country has the highest antelope diversity in Africa based on the pessimistic results (Figure 5-13 & Figure 5-4a). In agreement with the envelope approach, Aders' duiker is without suitable areas (Table 5-12), and only one unprotected cell provides suitable conditions for Weyns' duiker. A further four species (six in total) have less than the 20,000km^2 protection. There is an increase of three species (blue wildebeest, gerenuk [*Litocranius walleri*], and steenbok) with less than the 20,000km^2 protection compared to the present.

The steenbok and blue wildebeest exhibit large contractions (>96%), as does Weyns' duiker. At the opposite end of the scale Tanzania provides suitable conditions for the bushbuck (*Tragelaphus scriptus*) over more than 98% of the country (envelope and pessimistic approaches).

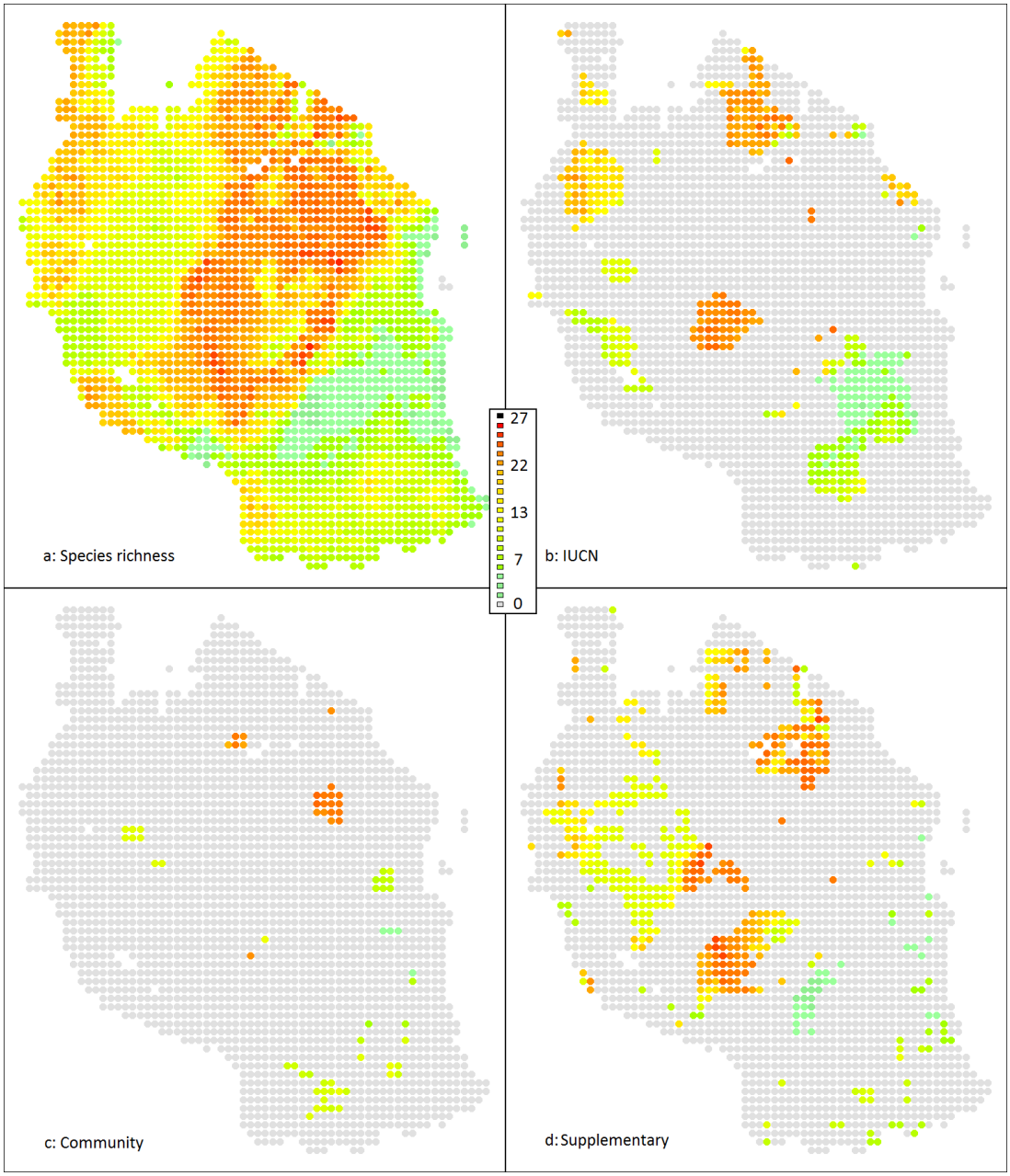

Figure 5-12: Species richness in Tanzania under the envelope approach, A1B climate scenario. a: presents the countrywide species richness; b: IUCN designated PAs; c: Community designated PAs; d: the remaining supplementary PAs. Each point represents a grid cell approximately 344km^2 at the equator.

Tanzania Envelope approach A1B climate scenario	Range within the Tanzanian PAN			Percentage of range within the Tanzanian PAN			Change in percentage of range within the Tanzanian PAN			Species range	
Species	IUCN PAs in 2080 (cells)	Community PAs in 2080 (cells)	Supplementary PAs in 2080 (cells)	IUCN PAs in 2080	Community PAs in 2080	Supplementary PAs in 2080	Change in IUCN PAs (present to 2080)	Change in community PAs (present to 2080)	Change in supplementary PAs (present to 2080)	Range in 2080(cells)	Percentage change (present to 2080)
Aders' duiker	0	0	0	0	0	0	0	0	0	0	-100
Weyns' duiker	0	0	0	0	0	0	0	0	0	1	0
Blue wildebeest	0	1	2	0	2.13	4.26	-11.45	-2.72	-19.75	47	-89.65
Steenbok	5	0	2	10.64	0	4.26	-3.94	-4.04	-19.41	47	-93.22
Abbott's duiker	7	0	2	19.44	0	5.56	4.06	0	-0.21	36	-65.38
Yellow-backed duiker	5	0	11	13.16	0	28.95	0	0	0	38	New
Salt's dik-dik	2	13	14	2.56	16.67	17.95	0	0	0	78	New
Bay duiker	21	1	32	9.72	0.46	14.81	0	0	0	216	New
Sitatunga	38	0	39	19.1	0	19.6	-1.86	0	0.55	199	-5.24
Black-fronted duiker	69	2	43	22.85	0.66	14.24	0	0	0	302	New
Guenther's dik-dik	54	36	92	7.37	4.91	12.55	0	0	0	733	New
Gerenuk	65	26	119	12.2	4.88	22.33	3.4	-7.21	6.94	533	192.86
Thomson's gazelle	101	25	112	18.67	4.62	20.7	2.44	2.28	-0.2	541	-57.8
Beisa oryx	83	27	149	11.72	3.81	21.05	1.24	-0.44	-1.75	708	7.6
Lesser kudu	98	29	154	13.37	3.96	21.01	0.61	0.14	-0.44	733	-3.55
Sharpe's grysbok	130	27	152	15.38	3.2	17.99	2.75	-1.11	-2.4	845	-51.46
Grant's gazelle	130	29	162	16.48	3.68	20.53	0.98	0.68	-0.27	789	-21.1
Mountain reedbuck	135	29	159	18.24	3.92	21.49	2.64	1.21	1.65	740	-33.27
Roan antelope	115	31	210	13.59	3.66	24.82	-4.05	0.36	-4.04	846	55.51
Hartebeest	128	33	203	13.87	3.58	21.99	-0.02	0	0.3	923	0.11
Klipspringer	153	28	184	15.33	2.81	18.44	-0.5	-0.83	-0.2	998	-56.34
Impala	147	29	192	15	2.96	19.59	-0.07	-0.89	0.39	980	-54.55
Eland	158	29	198	14.92	2.74	18.7	-0.88	-1.01	-0.04	1,059	-52.19
Kirk's dik-dik	161	30	215	15.75	2.94	21.04	0.53	-0.24	-1.32	1,022	-38.73
Blue duiker	255	28	159	21.72	2.39	13.54	2.14	-0.54	-1.2	1,174	-29.91
Oribi	162	39	249	15.1	3.63	23.21	-0.16	0.67	-1.6	1,073	17.78
Sable antelope	191	31	233	16.27	2.64	19.85	2.31	-1.43	0.56	1,174	-41.03
Greater kudu	193	30	237	16	2.49	19.65	1.33	-1.33	-0.12	1,206	-43.09
Southern reedbuck	200	40	239	15.87	3.17	18.97	-1.1	-0.78	0.6	1,260	-39.25
Harvey's duiker	221	38	246	16.9	2.91	18.81	-0.01	-0.54	0.66	1,308	-43.74
Topi	185	61	315	13.05	4.3	22.21	-2.54	0.68	-1.13	1,418	22.14
Natal red duiker	266	71	377	14.44	3.85	20.47	-2.39	-0.35	0.52	1,842	0.66
Suni	275	69	386	14.68	3.68	20.61	-2.44	0.01	2.06	1,873	-19.02
Common duiker	290	66	391	15.13	3.44	20.4	-1.66	0.11	2.06	1,917	-23.93
Bohor reedbuck	355	69	389	16.93	3.29	18.55	-1.5	0.13	0.08	2,097	-1.18
African buffalo	373	69	391	17.43	3.22	18.27	-0.21	-0.02	-0.27	2,140	2
Waterbuck	385	84	425	16.33	3.56	18.02	-0.62	0.08	-0.17	2,358	-5.53
Bushbuck	427	85	449	16.93	3.37	17.8	0.14	0	0.19	2,522	-1.06

Table 5-11: Protected area network coverage across Tanzania (envelope modelling approach under the A1B climate scenario) protected by IUCN designated PAs, community PAs, and supplementary PAs designations for each species. The table is ordered by the total number of protected cells (not shown) and by percentage change in species range (present to 2080). Red species have no protection under these predictions. Orange species have fewer than 59 cells protected (20,000km^2). Species which have "New" in the final column are new to the area. Percentage and change in percentage of the species' range is presented for each PA type.

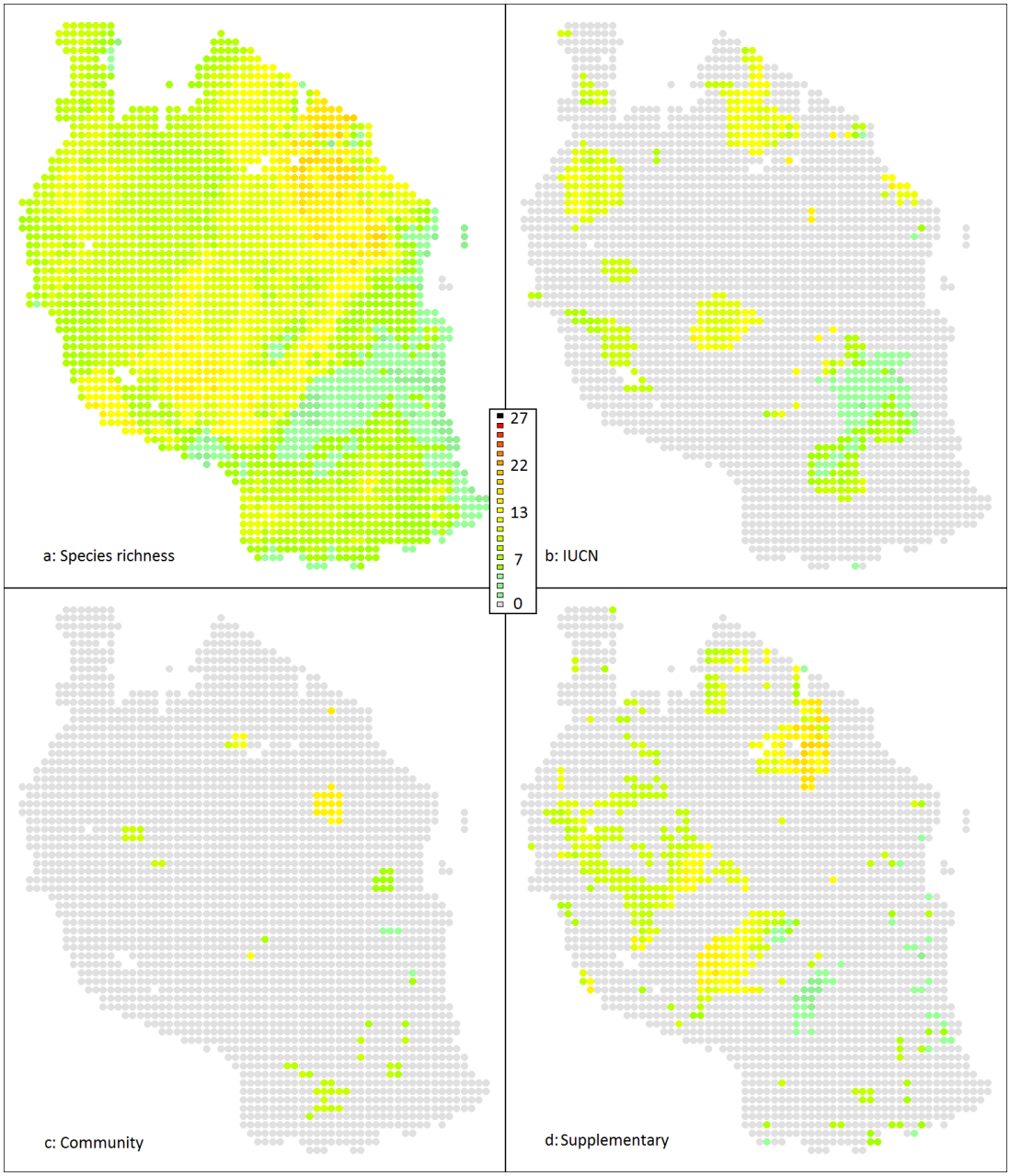

Figure 5-13: Species richness in Tanzania under the pessimistic approach, A1B climate scenario. a: presents the countrywide species richness; b: IUCN designated PAs; c: Community designated PAs; d: the remaining supplementary PAs. Each point represents a grid cell approximately 344km^2 at the equator.

Tanzania Pessimistic approach A1B climate scenario	Range within the Tanzanian PAN			Percentage of range within the Tanzanian PAN			Change in percentage of range within the Tanzanian PAN			Species range	
Species	IUCN PAs in 2080 (cells)	Community PAs in 2080 (cells)	Supplementary PAs in 2080 (cells)	IUCN PAs in 2080	Community PAs in 2080	Supplementary PAs in 2080	Change in IUCN PAs (present to 2080)	Change in community PAs (present to 2080)	Change in supplementary PAs (present to 2080)	Range in 2080(cells)	Percentage change (present to 2080)
Aders' duiker	0	0	0	0	0	0	0	0	0	0	-100
Weyns' duiker	0	0	0	0	0	0	-7.14	0	-3.57	1	-96.43
Blue wildebeest	0	1	0	0	7.14	0	-40.53	-0.4	-13.33	14	-97.54
Abbott's duiker	6	0	0	66.67	0	0	8.77	0	-15.79	9	-52.63
Steenbok	4	0	2	11.43	0	5.71	-6.25	-3.44	-16.1	35	-95.98
Gerenuk	7	20	22	5.04	14.39	15.83	-2.78	3.97	-6.57	139	-27.6
Natal red duiker	29	21	13	14.22	10.29	6.37	-9.61	5.24	-2.83	204	-63.18
Beisa oryx	13	21	30	7.6	12.28	17.54	-2.63	2.51	-3.39	171	-20.47
Sitatunga	33	0	36	17.74	0	19.35	-1.1	0	2.33	186	-32.61
Thomson's gazelle	56	21	40	34.36	12.88	24.54	8.43	4.8	1.64	163	-45.12
Mountain reedbuck	57	7	55	36.54	4.49	35.26	1.73	0.62	2.11	156	-13.81
Harvey's duiker	35	22	63	7.64	4.8	13.76	-0.59	0.49	2.38	458	-40.13
Southern reedbuck	50	11	66	19.23	4.23	25.38	-6.39	-0.94	3.59	260	-70.79
Sharpe's grysbok	45	1	88	14.2	0.32	27.76	-1.04	-3.47	4.37	317	-73.89
Lesser kudu	26	28	102	5.87	6.32	23.02	-1.21	1.11	-0.07	443	-17.5
Suni	55	43	69	9.52	7.44	11.94	-6.79	2.41	0.32	578	-52.39
Topi	87	17	95	37.18	7.26	40.6	-1.78	1.74	7.47	234	-28.22
Grant's gazelle	86	28	102	16.76	5.46	19.88	-0.21	0.53	-1	513	-12.9
Roan antelope	95	18	147	20.08	3.81	31.08	0.45	1.1	2.32	473	-52.61
Sable antelope	113	3	145	17.3	0.46	22.21	-0.8	-2.83	3.04	653	-63.62
Blue duiker	173	24	95	18.76	2.6	10.3	2.94	-0.26	-3.2	922	-37.11
Greater kudu	86	29	202	8.89	3	20.89	-5.57	-1.04	1.91	967	-54
Hartebeest	128	33	199	14.04	3.62	21.82	-4.83	-0.2	2.21	912	-59.98
Impala	145	29	189	15.43	3.09	20.11	-1.92	-0.42	1.71	940	-62.08
Klipspringer	152	28	184	15.28	2.81	18.49	-2.09	-0.68	0.04	995	-60.09
Oribi	126	27	216	15.56	3.33	26.67	-3.54	0.19	1.77	810	-42.06
Kirk's dik-dik	145	30	203	16.42	3.4	22.99	1.23	-0.14	-0.02	883	-34.88
Eland	154	29	195	15.16	2.85	19.19	-2.32	-0.69	0.54	1,016	-58.62
Bohor reedbuck	322	62	357	17.75	3.42	19.68	-0.03	-0.01	0.86	1,814	-24.98
Common duiker	290	66	391	15.13	3.44	20.4	-1.63	0.08	2.4	1,917	-25.81
African buffalo	370	68	387	18.25	3.35	19.09	0.58	-0.2	0.19	2,027	-17.27
Waterbuck	385	84	425	16.38	3.57	18.09	-0.37	0.21	0.09	2,350	-9.06
Bushbuck	427	85	448	16.95	3.37	17.78	0.19	0.01	-0.22	2,519	-2.48

Table 5-12: Protected area network coverage across Tanzania (pessimistic modelling approach under the A1B climate scenario) protected by IUCN designated PAs, community PAs, and supplementary PAs designations for each species. The table is ordered by the total number of protected cells (not shown) and by percentage change in specie's range (present to 2080). Red species have no protection under these predictions. Orange species have fewer than 59 cells protected (20,000km²).

Tanzania – Marxan solution

The PAN solutions (Figure 5-14 and Figure 5-15) require 19.2-23.9% of Tanzania's land mass to be protected (Table 5-8; 170,968-212,592km^2). The majority of the protection comes from existing IUCN PAs. However, 5.7-25.2% of existing community protection (1,720-7,568km^2; 5-22 cells) is utilized, in addition to 10,664-17,888km^2 of supplementary protection (31-52 cells). This leaves a requirement for 12,728-35,776km^2 (37-104 cells) of new protection which increases the PAN area by 3.8-10.6%.

All scenarios agree on the expansion of Selous game reserve (hereafter Selous) to the south east of the country. This large existing reserve, which currently protects an area of approximately 54,600km^2 (United Nations Environment Programme World Conservation Monitoring Centre, 2010), is enlarged. Under the pessimistic solutions the Selous expansion incorporates existing community PAs such as Tunduru to the south. All solutions include an expansion of Selous to the north with a new area of protection, and the HP pessimistic scenario continues this to the west linking the smaller IUCN areas of Mufindi Scarp and Kigogo Forest Reserve. Other areas are the expansion of Kilimanjaro and Mikomazi NPs on the north-east border. Under the pessimistic approach these are linked along the Tanzanian/Kenyan border and further linked to Tsavo West NP in Kenya. There is also expansion of the Serengeti NP and Ngorongoro Conservation Area. Expansion is required to the east of Serengeti under all scenarios. This area utilizes both community and supplementary PAs within the solutions. Under the HP pessimistic solution existing supplementary PAs and new PAs, between Ngorongoro and Kilimanjaro to the east, are required.

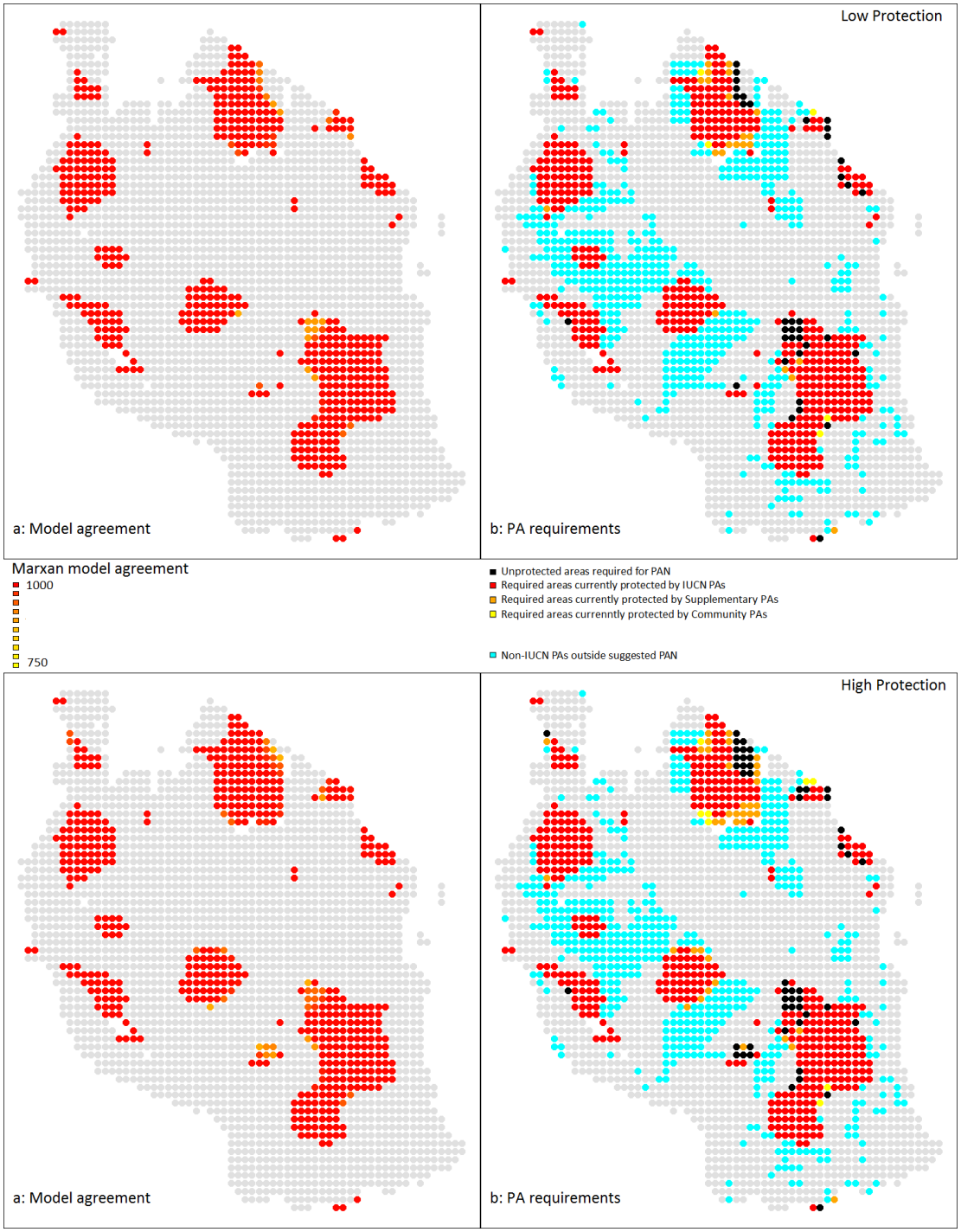

Figure 5-14: The envelope approaches Tanzanian component of the Marxan produced PAN without the habitat filter applied comparing the low(top) and high (bottom) protection options (see methods). a (left): The number of Marxan models agreeing (750 - 1000) from a 1000 repetition analysis. b (right): The current protected nature of the areas required for the PAN in (a). All IUCN areas are required in the future PAN suggesting a baseline PAN (red). Orange areas are currently protected by other organizations or groups. Yellow signifies areas under community management. Black areas are required for the PAN to complete coverage. Each point represents a grid cell approximately 344km^2 at the equator.

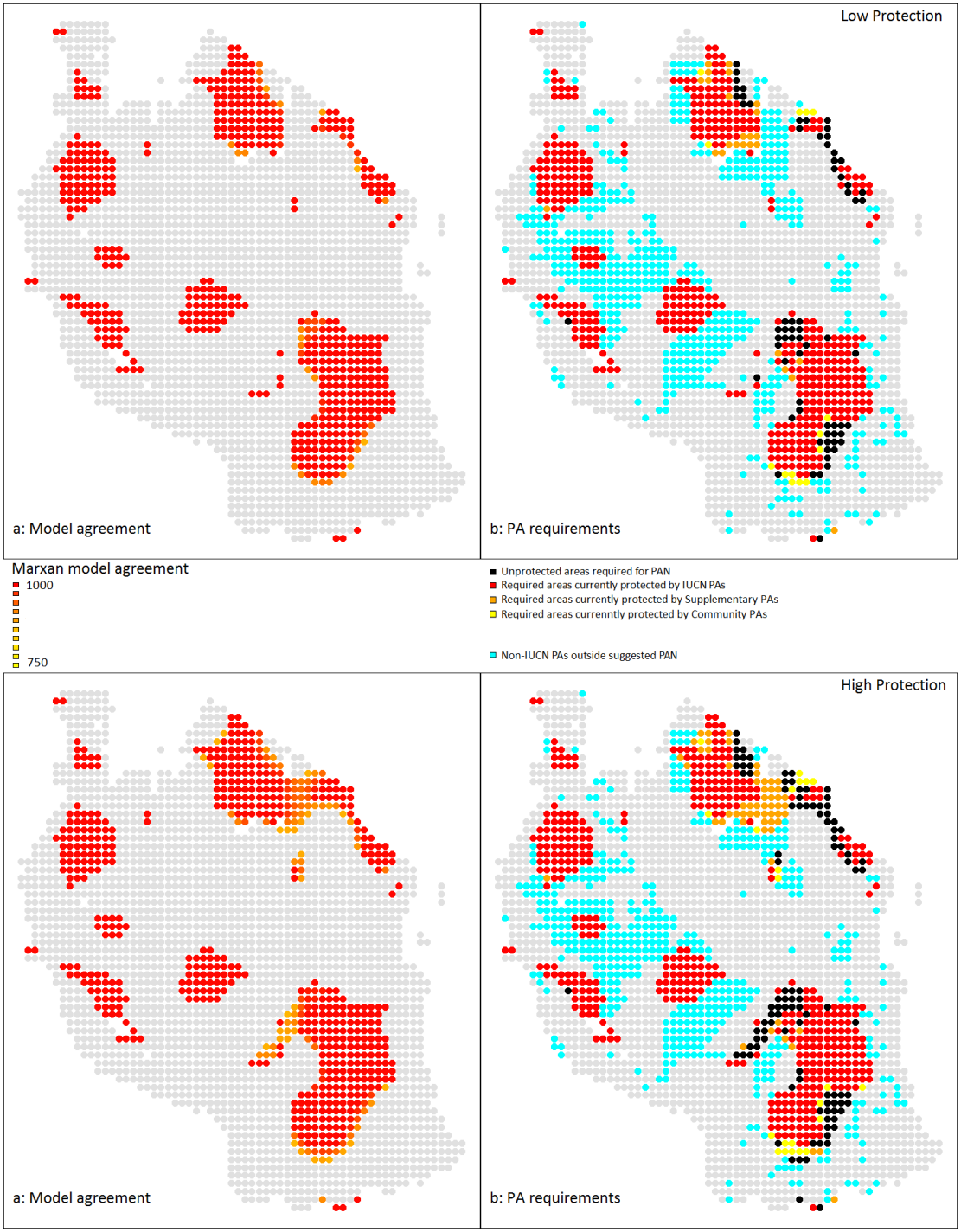

Figure 5-15: The pessimistic approaches Tanzanian component of the Marxan produced PAN without the habitat filter applied comparing the low(top) and high (bottom) protection options (see methods). a (left): The number of Marxan models agreeing (750 - 1000) from a 1000 repetition analysis. b (right): The current protected nature of the areas required for the PAN in (a). All IUCN areas are required in the future PAN suggesting a baseline PAN (red). Orange areas are currently protected by other organizations or groups. Yellow signifies areas under community management. Black areas are required for the PAN to complete coverage. Each point represents a grid cell approximately 344km^2 at the equator.

Namibia

40.2% of Namibia's cells (1,046 of 2,600; 375,992 of 894,400km^2) are either partly or fully covered by PAs (Table 5-4).

Namibia - envelope approach

Less speciose than Kenya or Tanzania, Namibia is predicted to have suitable conditions for 24 species in 2080 including four new species: Bohor reedbuck, Cape grysbok (*Raphicerus melanotis*), grey rhebok (*Pelea capreolus*), and nyala (Table 5-13).

The southern reedbuck is predicted to have a contraction of 99.7% in its Namibian range, and is only found outside of PAs. Sable and Sharpe's grysbok are also predicted to have very high range contractions (98.8% and 97.9% respectively). In 2080, a total of nine species have less than 20,000km^2 protection which represents an increase of seven from those at present. The additional species with low protection in 2080 include three of the new species (Bohor reedbuck, Cape grysbok, and grey rhebok), and four existing species (southern reedbuck, sable, Sharpe's grysbok, and southern lechwe).

The IUCN PAs in Namibia currently cover a smaller percentage of the country than in Kenya and Tanzania (Figure 5-16; Table 5-4), and do not offer protection in areas of high species diversity. Community and supplementary PAs are present in more species rich areas, but tend to be more fragmented in their distribution.

Namibia - pessimistic approach

Table 5-14 indicates that the sable, southern lechwe, Sharpe's grysbok, southern reedbuck, African buffalo, and the sitatunga are predicted to be without any suitable conditions in 2080. This represents a loss in species diversity of 27.3% (6 of 22 species) for the country. This is in contrast to the envelope approach where four of these species remain, albeit having small ranges. Four further species (10 in total) are predicted to have less than 20,000km^2 of protection, this represents an increase of one, the impala, from those at present.

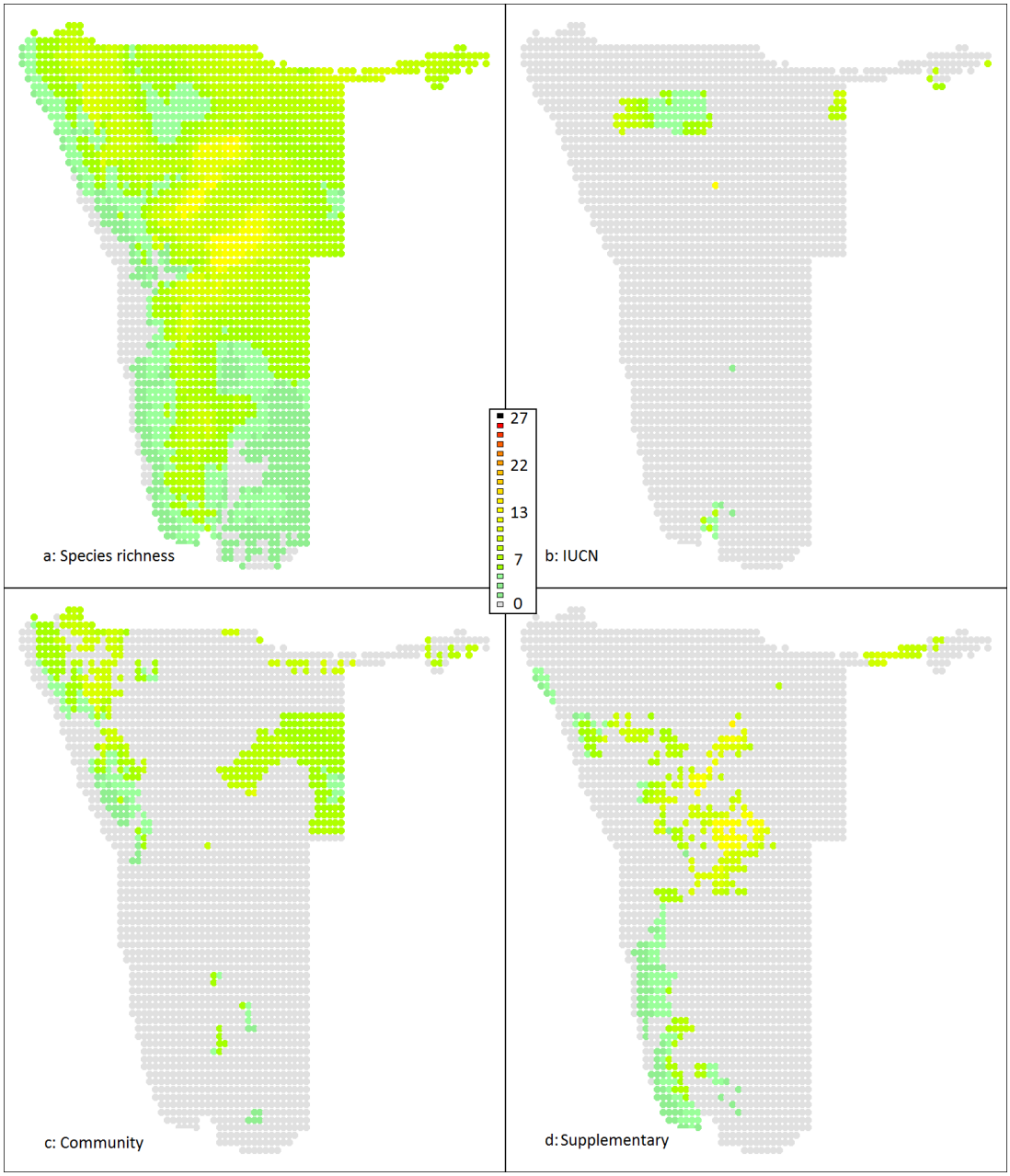

Figure 5-16: Species richness in Namibia under the envelope approach, A1B climate scenario. a: presents the countrywide species richness; b: IUCN designated PAs; c: Community designated PAs; d: the remaining supplementary PAs. Each point represents a grid cell approximately 344km^2 at the equator.

Namibia Envelope approach A1B climate scenario	Range within the Namibian PAN			Percentage of range within the Namibian PAN			Change in percentage of range within the Namibian PAN			Species range	
Species	IUCN PAs in 2080 (cells)	Community PAs in 2080 (cells)	Supplementary PAs in 2080 (cells)	IUCN PAs in 2080	Community PAs in 2080	Supplementary PAs in 2080	Change in IUCN PAs (present to 2080)	Change in community PAs (present to 2080)	Change in supplementary PAs (present to 2080)	Range in 2080(cells)	Percentage change (present to 2080)
Southern reedbuck	0	0	0	0	0	0	-5.19	-15.32	-9.61	1	-99.74
Sable antelope	0	0	1	0	0	20	-5.65	-16.22	11.15	5	-98.77
Sharpe's grysbok	0	0	3	0	0	37.5	-6.1	-12.47	29.28	8	-97.88
Bohor reedbuck	1	3	0	11.11	33.33	0	0	0	0	9	New
Cape grysbok	3	0	15	2.59	0	12.93	0	0	0	116	New
Grey rhebok	3	0	29	2.21	0	21.32	0	0	0	136	New
Bushbuck	3	18	21	3.41	20.45	23.86	-0.04	0.91	-0.27	88	1.15
Southern lechwe	1	0	42	1.27	0	53.16	-9.17	-24.92	47.78	79	-86.7
Waterbuck	7	22	20	3.5	11	10	1.5	-7	10	200	300
Oribi	9	30	21	4.76	15.87	11.11	1.86	-8.76	-3.38	189	173.91
Roan antelope	16	30	24	5.11	9.58	7.67	-0.23	-1.09	-0.87	313	11.39
Topi	21	48	73	4.45	10.17	15.47	-3.12	-14.23	3.57	472	-43.27
Impala	6	66	74	2.33	25.68	28.79	-6.56	-0.5	15.75	257	-74.6
Gemsbok	13	42	209	1.14	3.68	18.33	-3.84	-14.98	3.48	1140	-46.93
Hartebeest	53	124	91	8.01	18.73	13.75	0.9	-2.28	-0.16	662	-32.79
Eland	14	161	156	2.01	23.07	22.35	-4.42	2.49	8.06	698	-52.29
Springbok	11	107	252	1.17	11.35	26.72	-1.65	-9.27	8.69	943	-54.16
Kirk's dik-dik	20	213	150	3.07	32.67	23.01	-0.41	-0.7	4.16	652	-21.73
Blue wildebeest	52	257	174	4.65	22.99	15.56	-1.47	4.24	2.41	1,118	-27.21
Nyala	89	270	179	7.95	24.11	15.98	0	0	0	1,120	New
Steenbok	26	293	225	1.88	21.14	16.23	-2.95	2.08	3.69	1,386	-38.12
Common duiker	94	315	202	6.13	20.55	13.18	0.24	0	-0.11	1,533	-3.95
Klipspringer	34	300	361	2.49	21.95	26.41	-2.77	-0.96	8.5	1,367	-28.84
Greater kudu	92	404	232	5.26	23.11	13.27	-0.16	1.48	0.32	1,748	-0.23

Table 5-13: Protected area network coverage across Namibia (envelope modelling approach under the A1B climate scenario) protected by IUCN designated PAs, community PAs, and supplementary PAs designations for each species. The table is ordered by the total number of protected cells (not shown) and by percentage change in species range (present to 2080). Red species have no protection under these predictions. Orange species have fewer than 59 cells protected (20,000km^2). Species which have "New" in the final column are new to the area. Percentage and change in percentage of the species' range is presented for each PA type.

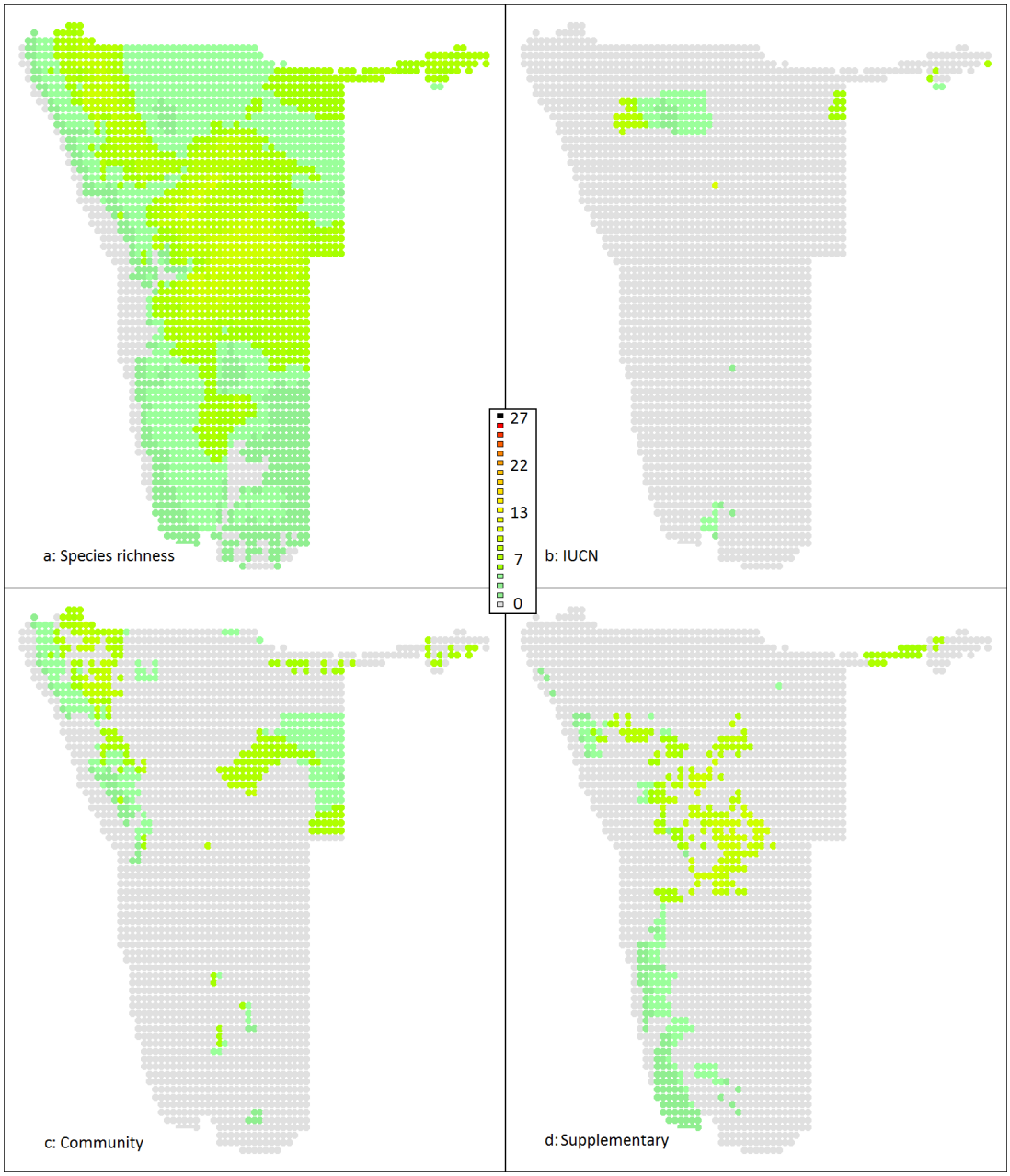

Figure 5-17: Species richness in Namibia under the pessimistic approach, A1B climate scenario. a: presents the countrywide species richness; b: IUCN designated PAs; c: Community designated PAs; d: the remaining supplementary PAs. Each point represents a grid cell approximately 344km^2 at the equator.

Namibia Pessimistic approach A1B climate scenario	Range within the Namibian PAN			Percentage of range within the Namibian PAN			Change in percentage of range within the Namibian PAN			Species range	
Species	IUCN PAs in 2080 (cells)	Community PAs in 2080 (cells)	Supplementary PAs in 2080 (cells)	IUCN PAs in 2080	Community PAs in 2080	Supplementary PAs in 2080	Change in IUCN PAs (present to 2080)	Change in community PAs (present to 2080)	Change in supplementary PAs (present to 2080)	Range in 2080(cells)	Percentage change (present to 2080)
Sable antelope	0	0	0	0	0	0	-8.33	-21.67	-35	0	-100
Southern lechwe	0	0	0	0	0	0	-10.64	-27.66	-19.15	0	-100
Sharpe's grysbok	0	0	0	0	0	0	-7.69	-23.08	0	0	-100
Southern reedbuck	0	0	0	0	0	0	-7.5	-18.5	-11	0	-100
African buffalo	0	0	0	0	0	0	-12.93	-27.59	-18.1	0	-100
Sitatunga	0	0	0	0	0	0	-8.2	-21.31	-34.43	0	-100
Waterbuck	1	5	0	5.88	29.41	0	-4.83	-2.73	0	17	-39.29
Oribi	2	12	4	5.88	35.29	11.76	0	0	0	34	0
Impala	1	34	0	2.04	69.39	0	-1.27	10.27	-11.6	49	-72.93
Bushbuck	3	15	21	4.41	22.06	30.88	-2.34	1.79	2.5	68	-8.11
Topi	15	29	21	9.26	17.9	12.96	0	0	0	162	0
Roan antelope	15	26	24	7.61	13.2	12.18	2.81	-12.12	0.64	197	-36.86
Hartebeest	38	63	69	8.5	14.09	15.44	1.83	-0.52	0.65	447	-61.79
Gemsbok	13	42	207	1.14	3.69	18.21	-3.18	-14.08	0.39	1,137	-54.06
Eland	14	110	145	2.36	18.55	24.45	-5.21	-2.06	9.56	593	-52.25
Kirk's dik-dik	17	211	106	3.51	43.6	21.9	-2.91	17.38	1.06	484	-49.05
Springbok	11	107	242	1.18	11.52	26.05	-2.89	-5.88	7.52	929	-60.97
Blue wildebeest	52	254	163	4.79	23.39	15.01	-1	3.58	3.74	1,086	-33.82
Steenbok	25	280	215	1.85	20.66	15.87	-2.85	1.89	1.7	1,355	-43.21
Klipspringer	28	249	273	2.51	22.31	24.46	-0.76	6.53	6.02	1,116	-32.53
Common duiker	94	314	202	6.19	20.67	13.3	1.58	2.21	-2.16	1,519	-37.54
Greater kudu	92	354	219	5.57	21.44	13.26	0.45	3.79	1.92	1,651	-21.64

Table 5-14: Protected area network coverage across Namibia (pessimistic modelling approach under the A1B climate scenario) protected by IUCN designated PAs, community PAs, and supplementary PAs designations for each species. The table is ordered by the total number of protected cells (not shown) and by percentage change in species range (present to 2080). Red species have no protection under these predictions. Orange species have fewer than 59 cells protected (20,000km^2).

Namibia – Marxan solution

40.2% of Namibia's area currently has some form of protection. However, the PAN solutions (Figure 5-18 and Figure 5-19) require only 5.1-6.2% of the country's area (45,752-55,040km^2; 133-160 cells; Table 5-8). The protection is provided largely by existing IUCN PAs. Only 1.5% of existing community protection is utilized (7 of 472 cells), mostly from the Caprivi Strip to the north-east of the country. The Marxan solution also requires a small area of existing supplementary protection on the Caprivi Strip (1,376km^2; 4 cells), and new PAs (688-1,032km^2; 2-3 cells). In the south of the country and on the western border with Botswana and South Africa, the Marxan solution utilizes a further 688-1,720km^2 (2-5 cells) of supplementary protection, as well as 3,096-10,664km^2 (9-31 cells) of new protection. The areas in the far south of the country expand Ai-Ais Hot Springs NP, while the new area bordering Botswana and South Africa expands the Kgalagadi Transfrontier Park (this is not part of the envelope LP solution).

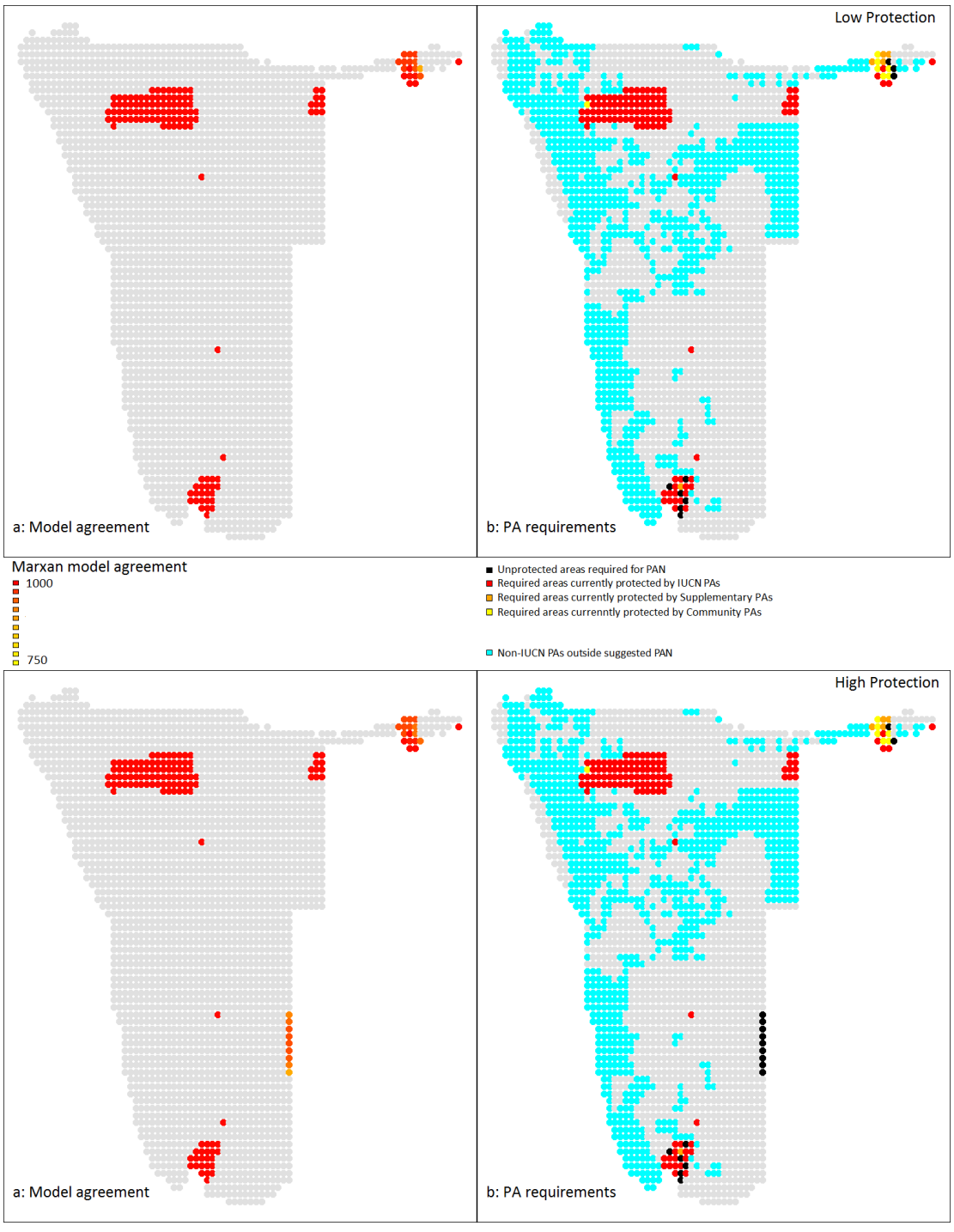

Figure 5-18: The envelope approaches Namibian contribution to the Marxan produced PAN without the habitat filter applied comparing the low(top) and high (bottom) protection options (see methods). a (left): The number of Marxan models agreeing (750 - 1000) from a 1000 repetition analysis. b (right): The current protected nature of the areas required for the PAN in (a). All IUCN areas are required in the future PAN suggesting a baseline PAN (red). Orange areas are currently protected by other organizations or groups. Yellow signifies areas under community management. Black areas are required for the PAN to complete coverage. Each point represents a grid cell approximately 344km^2 at the equator.

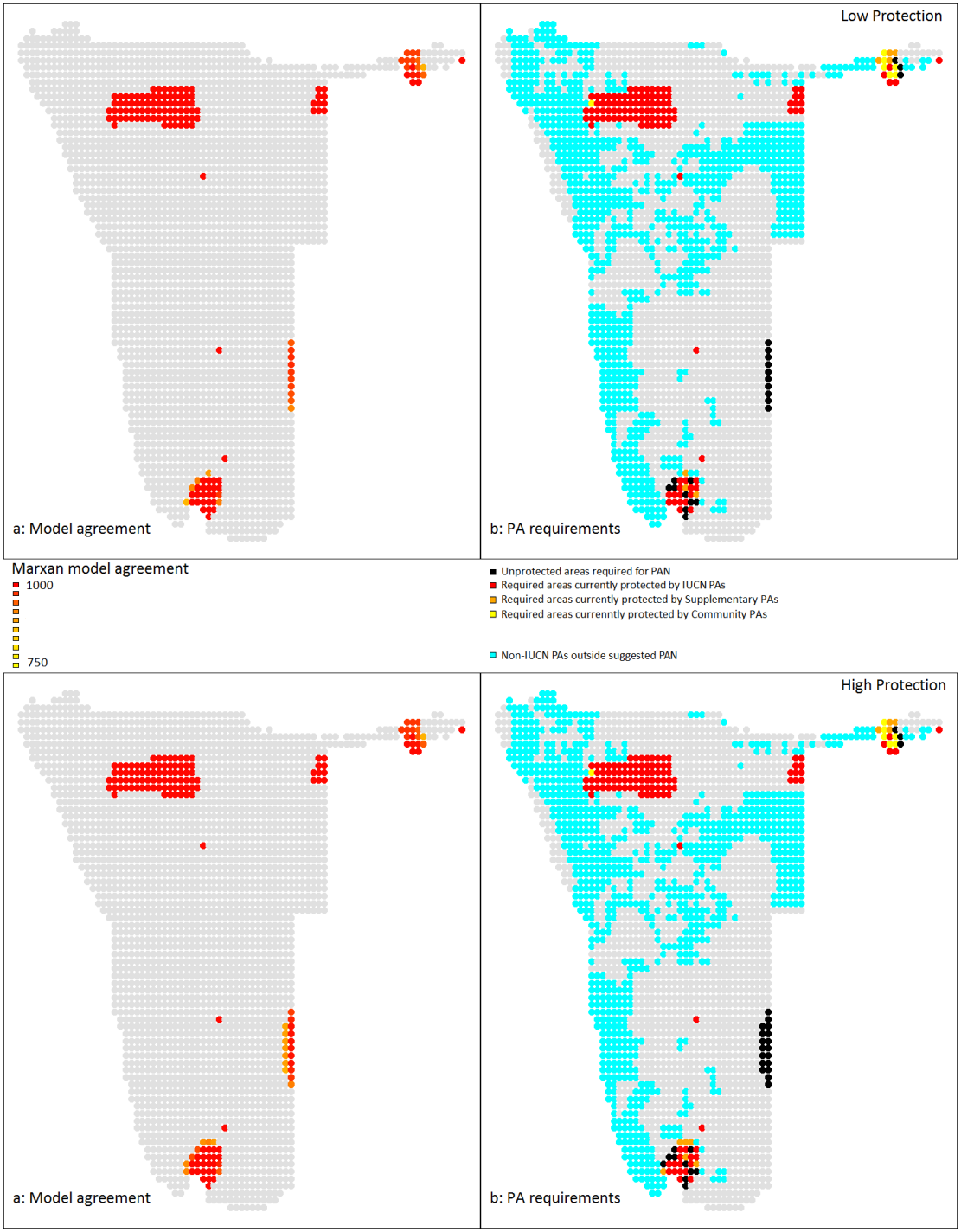

Figure 5-19: The pessimistic approaches Namibian contribution to the Marxan produced PAN without the habitat filter applied comparing the low(top) and high (bottom) protection options (see methods). a (left): The number of Marxan models agreeing (750 - 1000) from a 1000 repetition analysis. b (right): The current protected nature of the areas required for the PAN in (a). All IUCN areas are required in the future PAN suggesting a baseline PAN (red). Orange areas are currently protected by other organizations or groups. Yellow signifies areas under community management. Black areas are required for the PAN to complete coverage. Each point represents a grid cell approximately 344km^2 at the equator.

Change in proportion of species ranges covered by protected areas

Table 5-15 summarizes the importance of different PA types in the future assuming no change is made to the PAN. The general trend is a reduction in the percentage of species ranges being protected in the future compared to present. Under the pessimistic approach, the average percentage of a species range which is protected by IUCN PAs decreases by 1.1% between now and 2080. For non-IUCN PAs the drop is very small (0.2%). This trend is reversed using the envelope approach. Here the average reduction in species range being protected by IUCN PAs increases by 0.4% whereas non-IUCN PAs reduce by 0.9%. However, as above, the difference is small.

		Mean percentage of species ranges protected by the existing PAN in 2080			Mean change in the percentage of species ranges protected by the PAN between present and 2080		
	Approach	IUCN PAs	Community PAs	Non-IUCN (Africa)/ Supplementary PAs (KNT)	IUCN PAs	Community PAs	Non-IUCN (Africa)/ Supplementary PAs (KNT)
Africa	Pessimistic (n_s=73;n_e=69)	10.64 s.d.±14.80	NA	10.75 s.d.±7.95	-1.11 s.d.±3.06	NA	-0.16 s.d.±5.84
	Envelope (n_s=73;n_e=72)	8.81 s.d.±10.90	NA	8.20 s.d.±4.94	-0.35 s.d.±3.97	NA	-0.88 s.d.±2.53
Kenya	Pessimistic (n_s=34;n_e=30)	12.44 s.d.±18.66	2.30 s.d.±1.62	12.18 s.d.±18.85	2.61 s.d.±19.15	0.1 s.d.±1.45	1.63 s.d.±12.38
	Envelope (n_s=33;n_e=39)	7.70 s.d.±5.70	2.62 s.d.±1.60	10.85 s.d.±15.26	-1.38 s.d.±5.13	0.14 s.d.±1.53	1.14 s.d.±2.26
Namibia	Pessimistic (n_s=22;n_e=16)	4.54 s.d.±2.60	24.20 s.d.±15.24	15.98 s.d.±8.47	-1.28 s.d.±2.33	0.63 s.d.±7.64	1.37 s.d.±4.64
	Envelope (n_s=20;n_e=24)	3.52 s.d.±2.78	14.56 s.d.±10.95	18.61 s.d.±11.31	-2.46 s.d.±3.03	-5.88 s.d.±8.15	7.12 s.d.±12.52
Tanzania	Pessimistic (n_s=33;n_e=32)	17.04 s.d.±12.43	4.48 s.d.±3.71	18.62 s.d.±9.37	-2.71 s.d.±7.92	0.32 s.d.±1.94	-0.77 s.d.±5.38
	Envelope (n_s=33;n_e=37)	14.22 s.d.±5.03	3.18 s.d.±2.70	17.90 s.d.±5.92	-0.34 s.d.±2.85	-0.54 s.d.±1.64	-1.19 s.d.±5.13

Table 5-15: Effectiveness of PAs for Africa and by country (Kenya, Namibia, Tanzania [KNT]). The average PAN coverage percentage of all present species is split by PA type. The average coverage change from the present to the 2080 time period is similarly split. Community PAs were not separately assessed for Africa and are included within the "Other PAs" group. n_s is the number of species currently resident in the PAs, or where suitable climate exists (envelope approach). n_e is the number of species present at 2080. This number can fall where species go extinct, or rise with immigration of new species (envelope approach only). Envelope deviation values are provided.

In Kenya, under the pessimistic approach, there is a positive change of 2.6% for IUCN PAs indicating they could become more important for species protection, as could the supplementary PAs.

In Namibia, where there is more community and supplementary PA coverage, under the envelope approach there is a fall in the protection provided by IUCN and community PAs, but this is compensated by increases in protection provided by the supplementary PAs.

Tanzania shows a general trend of less protection being provided by PAs in the future across all PA types and approaches, however, most of the changes are small.

Discussion

Climate change (CC) is one of many threats facing antelope species globally. While some of the threats, such as civil unrest, are localized and may be short-term, the impact of CC is global and expected to rapidly increase over the next century (MEA, 2005). CC has the potential to cause extinction (Foden *et al.*, 2009; Carpenter *et al.*, 2008; Thuiller *et al.*, 2005b; Thomas *et al.*, 2004;), and identifying those species at risk is the first step in providing mitigation and protection against the threat. The results presented in chapter four identified the hirola as having no connected viable areas of climatic suitability at the end of the 21st century under either the envelope or pessimistic scenario. Under the pessimistic approach, where dispersal is prohibited, the addax, Aders' duiker, and the Nile lechwe also have no climatically suitable areas by 2080. This represents a loss of 5% of African antelope species. In this study, a further 5% are left without any protection via PAs (pessimistic scenario: silver dik-dik, dibatag, Speke's gazelle, and beira). If we make the conservative assumption that species are only viable if protected by PAs, a further 8 species are rendered vulnerable through their range size being limited to less than 20,000km^2 (within PAs). In total 16 species (22%) may be extinct or threatened in 2080 through the impact of climate change and lack of protection based on the A1B climate scenario using these measures. Twelve of those species are already threatened through other IUCN measures (IUCN, 2014a). For those species CC is making an already uncertain future even bleaker.

In addition to those species threatened by climate change or lack of protection, a further 10 species (14%) are currently threatened by other factors (IUCN, 2014a). Assuming no change in threat status before the end of the century, this would result in 26 species (36%) being threatened or extinct under the pessimistic approach by 2080 (under the envelope approach this would be 24 species). This may seem a highly pessimistic view of the future, but as the projected human population quadruples to 4.18 billion in Africa in 2100 (United Nations, 2014), the threat from humans is likely to grow (Lindsey *et al.*, 2013) as population growth leads to encroachment of wildlife areas (Kiringe *et al.*, 2007). This being the case, protected areas may become the only sites where viable populations exist.

Under the envelope approach, Kenya, Tanzania, and Namibia, are all predicted to have increased species richness through immigration of species. Under the envelope approach Kenya gains seven species and loses the hirola; Tanzania gains five, but loses the Aders' duiker; Namibia gains four, but three have their ranges reduced by over 97%. The majority of Kenya's and Tanzania's immigrant species are predicted to have global ranges that are

contracting or remaining stable. This suggests that their ranges are shifting to these areas rather than expanding. The increasing number of species suggests that gamma diversity for these countries (i.e. landscape diversity) has the potential to be higher based on climate, and further highlights the importance of Kenya and Tanzania in particular, to antelope conservation. If the pessimistic approach is followed Tanzania remains the most antelope diverse area in Africa in spite of the loss of the Aders' duiker, and a further three species exhibiting losses of >90%. Kenya, despite losing four species and two further with >90% losses, remains a country with high antelope diversity compared with the rest of Africa.

Reviewing these three countries, there are clear differences in the way PAs are apportioned within each country's PAN. Each country has more than the African average PA allocation (Africa 14.3%), although this varies greatly by country. Namibia has the highest community PA provision by some margin (18.2% land mass compared with Tanzania's 3.4% and Kenya's 1.9%). It also has high supplementary PA allocation, similar to Tanzania, but the lowest IUCN share. The high percentage of community PAs is due to Namibia's political changes and decisions in the 1970s that promoted the private protection of wildlife areas, which led to new sources of revenue and economic gains (Jones & Weaver, 2009). Therefore the prediction that 27% (6 species) of the country's antelopes could be lost under the pessimistic approach, is a worrying statistic not just for conservationists, but for the many that base their livelihoods on wildlife. However, suitable conditions are present for four of those species, albeit in small areas under the envelope scenario. This may present an opportunity for translocation of those species if they are unable to disperse naturally.

Kenya is renowned for its wildlife and nature tourism and high species diversity. Despite this, of the three countries, it has the lowest percentage allocation of PAs (15.4%) with a focus on IUCN PAs (48.3% IUCN, 12.5% community, 39.2% supplementary). Tanzania has a high allocation of land mass to PAs (38%) and shares Kenya's focus on IUCN and supplementary PAs over community PAs (44% IUCN, 8.8% community, 47.2% supplementary). Considering the high levels of diversity in both countries and the comparable importance of travel and tourism to GDP for all three countries (see Figure 5-20: World Travel and Tourism Council, 2014), increasing the PA allocation in Kenya may present benefits on many levels.

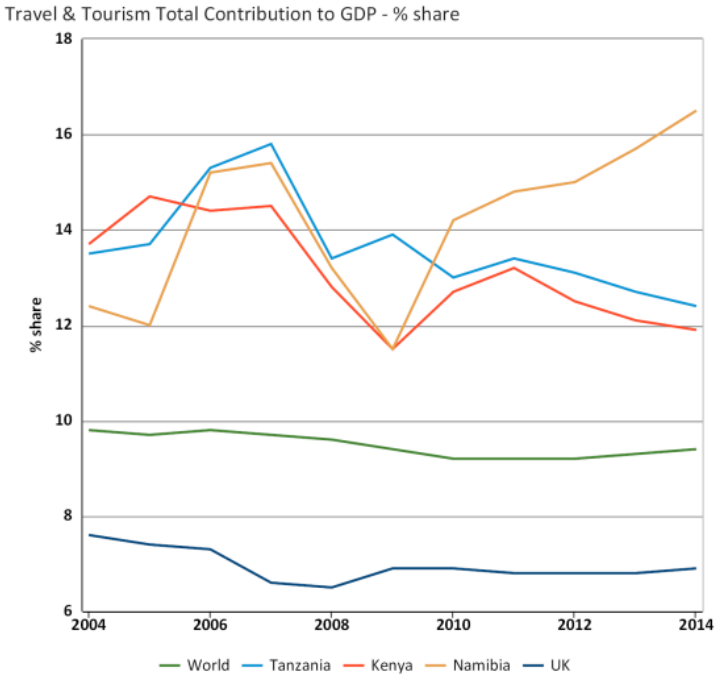

Figure 5-20: The contribution of travel and tourism to gross domestic product (GDP) for Namibia, Kenya, Tanzania, UK and World (World Travel and Tourism Council, 2014).

PAN recommendations

Systematic conservation planning consists of a number of steps (from Margules & Pressey, 2000):

1. Compile data on biodiversity in the conservation planning area
2. Identify conservation goals for the planning region
3. Review existing conservation measures
4. Select additional conservation areas
5. Implement conservation actions
6. Maintain the required values of conservation areas

Here, the PAN solutions presented address the first four of these steps for Africa's antelopes. Step five includes the assessment of specific areas in terms of suitability and the ability to protect those areas. If areas are deemed unsuitable step four is returned to. The solutions presented were based on the areas that Marxan most commonly identified as part of a valid solution, where 750 agreed those areas were important out of 1,000 solutions produced. Therefore the remaining solutions may present alternatives if required. Alternatively new

solutions can be generated after removal of unsuitable areas. Below I review the solutions for each of the geographic regions.

Africa:

The PAN recommendations to adequately protect all antelope species in Africa require 8.1-8.7% of Africa's land mass (7,320-7,776 cells; 2,518,080–2,674,944km^2). This protects an area greater than 20,000km^2 for all species where possible; ensuring they would not be classified threatened under the IUCN spatial guidelines. Other threats would then have to be assessed. Therefore, to protect a single group of mammals requires approximately half of the 17% Aichi land area target in Africa (CBD, 2010), to accommodate their needs. However, by protecting antelopes a wider group of species from other taxonomic groups will also be protected, i.e. antelopes can act as umbrella species (Roberge & Angelstam, 2004; Caro, 2003). Antelopes are a wide ranging, highly diverse group of species that live in a multitude of different environments and ecosystems from desert to tropical rainforest (Estes, 1991). Predators focusing on antelopes, such as large cats and spotted hyaena (Estes, 1991), have similar ranges as these are linked/constrained through a common food web (Holt & Barfield, 2009). Therefore, species that have antelope in their food web, may benefit from protection via an antelope centred PAN. Still, this is no guarantee of adequate protection of the wider ecosystem as the needs of each species vary and the use of large mammals as umbrella species has had limited success (Roberge & Angelstam, 2004; Caro, 2003). Therefore, by protecting 8.1-8.7% of Africa based on minimum antelope requirements does not infer protection for all of Africa's biodiversity to the same level. Further analysis of a wider range of taxa would be required to understand how much of Africa's area would need to be protected to encompass all biodiversity.

Both the high and low protection (HP, LP) scenarios under the envelope approach require less area protected than under the pessimistic approach, but species under the envelope approach have larger ranges and therefore require greater area to be protected per species. These two facts seem at odds, however, under the envelope approach the ranges of all species being larger means that there is greater overlap between species ranges. Therefore protecting one cell under the envelope approach is likely to protect more species than under the pessimistic approach, ultimately reducing the number of cells required under the envelope approach. This being the case, if species are able to disperse unhindered the cost and size of the required PAN would reduce. However, an environment whereby species

could move unhindered would suggest a great reduction from human pressures that would likely influence the specification of that PAN.

The HP scenario provides a similar looking PAN to that of the LP except for expansions and widening of connectivity between protected areas. The Marxan software generates best fit PAN solutions according to the set targets and costs. In this study there was no restriction on the costs of developing the PAN. To establish costs requires detailed understanding of each land unit in the prospective area. This is not readily available for the entire African continent at the scale used here. For that reason the major cost implemented here was a high tariff on boundary length which produces solutions with larger connected PAs, rather than localized or fragmented PAs. Larger PAs are indeed the preferred option by conservationists (Hannah, 2008; Halpin , 1997; Diamond, 1975) as these help support larger populations which retain a broader gene pool and natural behaviour such as migrations, at a lower cost per unit area through economies of scale (Di Minin *et al.*, 2013; Bruner *et al.*, 2004). In addition, larger PAs reduce the likelihood of species extinction within those reserves (Brasheres *et al.*, 2001). The widening of connecting corridors is accompanied by a recommendation for the expansion of existing IUCN areas. Connecting two areas via a wide corridor can be more computationally cost effective than expanding areas alone depending on the shape of the pre-existing PAs, the distance between them, and the species that are present within the corridor. Connecting areas brings additional advantages such as allowing population expansion, protecting dispersal routes, and allowing species to track climate change or return to areas of human caused extirpation, and ensuring the spread of new genes to existing populations (Bennett, 2003). This assumes that any fences between neighbouring PAs can be removed to ensure free movement of animals.

Large PAs provide many benefits, however, there are also benefits of having multiple reserves protecting each species. The debate between single large or several small (SLOSS) was discussed in detail in the 1970s (Shafer, 2001; Diamond, 1976; Simberloff & Abele, 1976). A key argument for multiple reserves is protection from stochastic or catastrophic events, either human or natural, that have the potential to threaten populations within a single reserve. Disease, fire, and human conflict potentially threaten entire species if located in a single reserve (Bennett, 2003). However, compromise is required to balance the need for multiple sites and the need for large sites to ensure minimum area requirements for species with the conservation funds available. A factor that may conflict with the argument for large reserves is also the requirement to protect all species as in the case here. Protecting species

that are found in limited areas may require the development of small reserves focused on those species. These areas may protect other species and may lend themselves to being part of a larger PA, however, if they are in areas of low antelope diversity this may result in small fragmented PAs being suggested as part of a rule based solution as presented here. An example in the solutions presented here are the new areas in Somalia to protect beira, Speke's gazelle, dibatag, and silver dik-dik that are without existing IUCN protection.

There is relatively low utilization of non-IUCN PAs in the final solutions. This is due to these PAs tending to be smaller, fragmented, and having less connectivity to IUCN PAs. The assigned cost of non-IUCN PA cells is the same as all the remaining cells (i.e. cells with no protection). Therefore, if two cells contain the same species, and one is adjacent to an IUCN PA cell while the other is not, the adjacent cell is considered more cost effective, due to a shorter boundary, regardless of existing protection. The result is that the non-IUCN PAs that are utilized are those that aid in the expansion and/or connection of IUCN areas rather than being standalone sites. This can be clearly seen in the south east of Africa (see Figure 5-21).

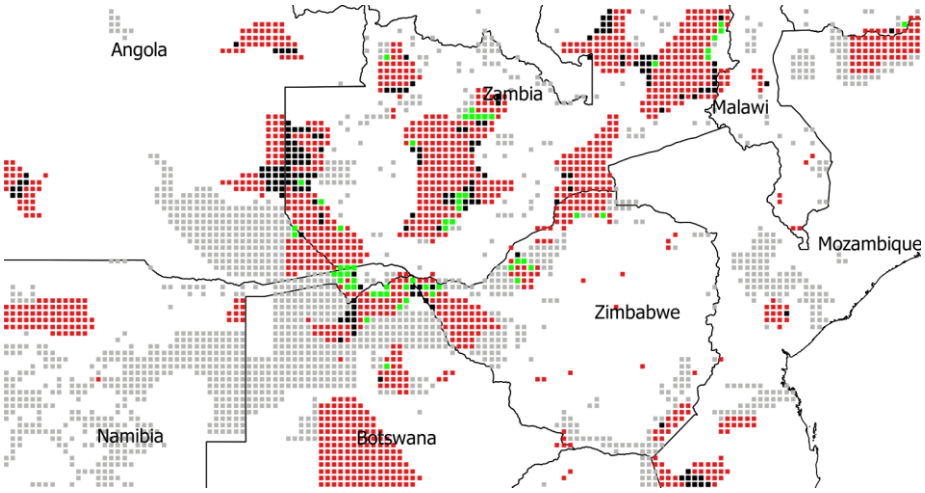

Figure 5-21 : Expanded view of central southern Africa highlighting the utilization of non-IUCN PAs (green areas) to interconnect IUCN areas (red). Additional areas required are black. Light grey areas are existing non-IUCN PAs not included in the PAN solution. Data are from the envelope high protection solution. Each point represents a grid cell approximately 344km^2 at the equator.

The future PAN solutions are based around the existing IUCN PAN. This was chosen because IUCN designated areas were considered more likely than the non-IUCN PAs to still be present at the end of the century: given the human pressures on land it is unclear how non-IUCN PAs will change in the future. Community PAs, included within non-IUCN PAs at the continental scale, have shown variable success (Measham & Lumbasi, 2013; Kellert *et al.*, 2000) and could therefore be considered vulnerable. Community PAs may also include limited term projects, for example 20 years for forest carbon preservation, and it is unclear what will

happen at the end of those contracts (Namirembe *et al.*, 2014). Farming and development demands could influence land owners to change their objectives and goals. In addition, current private PAs (also included within non-IUCN PAs) may have management goals not necessarily allied with greater conservation objectives, such as hunting. Further, fences may be in place around private areas that may prove difficult to remove given those goals. Finally, not all private and community PAs are in the WDPA (Dudley, *et al*., 2014) perhaps signifying a lack of commitment to a wider coordinated conservation effort. While this may seem an overly cautious approach given that some of the other areas are as well established as the IUCN PAs (for example, Ramsar, UNESCO Biosphere Reserves, and World Heritage Sites), as the world's largest environmental organization (IUCN, 2014b) an IUCN designation typically characterizes more established PAs.

Kenya

Kenya is an area of very high antelope diversity both presently and in the future. Kenya's current PAN requires expansion of up to 15.3% to fulfil continent-wide solutions (27 - 39 cells; 9,288-13,416km^2). This expansion represents an increase of up to 2.4% of Kenya's land mass. The Tsavo East and West expansion, connecting to Tanzania through to the Serengeti (HP pessimistic), forms the largest PA grouping in the country. It utilizes IUCN, community and supplementary PAs that are on the border with Tanzania to create the suggested transfrontier park. On the northern border with Ethiopia, further inter-country parks are suggested linking the Ethiopian PAs of Chelbi and Murle with Kenya's Lake Turkana National Park. While new areas are important for the PAN, only up to 20% (range 5-20%) of supplementary PAs and 3.1% of community PAs are utilized in the solutions. The reason for this is that many of these PAs have no direct connection to IUCN reserves and the Marxan software was configured to preferentially select adjacent areas as described above. This does not mean these areas are not important when considering the wider conservation effort and the preservation of all biodiversity.

Tanzania

Tanzania requires an additional 1.4 - 4.0% of the country's area be established as protected areas (additional 37 - 104 cells; 12,728-35,776km^2). This represents a 10.6% increase in the size of the existing PAN, and is the largest increase in area required of the three countries assessed. In total 19.2 - 23.9% of Tanzania should be protected as part of an antelope-centric PAN. This reaffirms the importance of the country for antelope conservation. The PAN suggestions are similar between pessimistic and envelope approaches with the HP scenario

extending areas highlighted under the LP scenario. Tanzania has greater utilization of the current community and supplementary PAs than Kenya or Namibia. In particular their utilization is found in PAs bordering Selous game reserve, Serengeti NP and Ngorongoro conservation area in the north. Under the HP pessimistic approach large expanses of PA are established incorporating community, IUCN and supplementary PAs between Tanzania and Kenya. The expansion along the north eastern borders of Tanzania link with Kenya and encourages the creation of a transfrontier park to provide protection to species as they disperse between these countries. Under the pessimistic HP scenario this transfrontier park would cover an area of approximately 98,000km^2.

Tanzania has, and is predicted to have, the most species rich areas for antelopes in Africa. However, despite the solutions requiring large areas for antelope conservation, many of the species rich areas in central Tanzania are not widely incorporated in the solutions outside of the existing IUCN PAs. This appears to be a mistake or a missed opportunity to protect multiple species; however, the reason is due to the large number of common species predicted to be found across that area with no vulnerable species found in highest diversity areas. This being the case, these species are adequately protected in existing IUCN areas, or those areas that have been locally expanded. High diversity areas may however present other opportunities. When planning PANs where ecotourism is required to fund areas, it may be important to readjust the parameters and encourage areas such as these where visitors could potentially see more species.

Namibia

The PAN suggestions require 5.1-6.2% of Namibia's area (133-160 cells; 45,752-55,040km^2) to be protected as part of the network. This includes 7 community (less than 1.5% of all community PAs) and 5-8 supplementary PA cells that are largely focused on the Caprivi Strip in the north of the country. The Caprivi Strip forms part of an important corridor between Angola and Zambia to the north, and Botswana to the south. This is the area of highest antelope diversity in Namibia and is also the focus of new areas that expand the Caprivi Strip corridor between the countries. The area is an important component of the proposed Kavango-Zambezi Transfrontier Conservation area (KAZA) that seeks to link five countries. The Caprivi Strip is important both for migrating and dispersing species, such as African buffalo that display seasonal movements between countries, and the livelihoods of the locals through nature-based tourism (Naidoo *et al.*, 2012). This area should therefore be considered of great importance to species dispersing due to climate change in the future.

Being a non-IUCN PA dominated area this is a clear example of how community and supplementary PAs contribute to a wider African PAN, and the need to preserve and incorporate them.

The Caprivi Strip, and the new area required on the eastern border with Botswana and South Africa that would extend Kgalagadi Transfrontier Park into Namibia, bring into focus another core problem of international borders and fences that present barriers to natural dispersal and migration. Naidoo *et al*. (2012) describe how buffalo in Namibia have to "funnel" through a 20km wide gap in the fences between countries. This is believed to ultimately reduce dispersal between countries. This emphasizes the fact that, even with routes between international borders, species may be slowed in their dispersal throughout Africa. In the future it would be possible to expand the Marxan configuration to highlight known areas of importance for dispersal making them a required component of the PAN as with the IUCN PAs in this study.

The low PA requirement across Namibia is largely due to low diversity of species, and the widespread nature of many of the remaining species allowing their protection elsewhere. The Marxan PAN suggestions above require less than 6% of the country set aside compared to the 40% currently assigned. This does not suggest that the other areas are superfluous. They provide additional protection to many species including antelopes, but additionally they are a source of income to local people, contribute greatly to national gross domestic product (GDP), and help educate visitors to the need for conservation. In 2013 travel and tourism accounted for 14.8% of Namibia's GDP and is forecast to rise to 22.2% by 2024 (WTTC, 2014). In Namibia, nature and wildlife tourism dominates the travel and tourism contribution to GDP (Muchapondwa & Stage, 2013). The 2013 figure is second highest in Africa behind Madagascar (15.9%), and higher than Kenya (12.1%) and Tanzania (12.9%), with the continent average being 8.5% (WTTC, 2014). This emphasizes the difficulty and importance of marrying conservation planning with national and international socio-economic drivers. However, the PAN solutions presented here focus solely on providing cost effective solutions to conserve Africa's antelopes.

Summary

Each of the three countries assessed highlights multiple areas where the PAN solutions require international agreements to develop or expand existing transfrontier parks. If there is a global will to protect biodiversity, these solutions demonstrate that this cannot be accomplished where geographic regions are divided by fences or political barriers.

International coordination is required to establish transfrontier parks that enable population dispersal, but also protect and preserve each nation's sovereignty and human population.

The effect of range shift on PAN coverage

It is important to understand the impact that a shift of species range, due to climate change, will have on how well the existing PAN provides protection. Climate change may cause a species' range to contract, expand, and shift, or any combination of those. Any change in a species' range may affect the percentage of range that is protected in the future. However, the percentage of range that is protected, or the change in percentage of range protected, may be misleading as these values need to be related to the species' previous protection status and the type of range change occurring, i.e. contraction, expansion, or shift (See Table 5-16).

Change in range based on number of cells	Effect if a species is currently largely protected by the PAN	Effect if a species is currently largely unprotected by the PAN
Contraction	Contraction will likely increase the percentage protection for the species, albeit the absolute area of protection is reduced. The positive message of raised protection hides the negative implications of the contraction of range.	There is likely to be little effect on the percentage of range protected. Here the percentage change between the present and the end of the century alone may not highlight the plight of a species.
Expansion	Expansion of potential range is positive for the species, but may result in a reduction of the percentage of range protected as the range expands beyond current PAN provision.	Protection is more likely to increase if the expansion of range results in species dispersing into PAs. This is the most positive scenario for species if there is no change in the existing PAN. However, the percentage of range protected may show little change as the absolute range size increases.
Shift	A shift in range may result in the species dispersing outside of protected areas causing a fall in percentage protection. This reduction in percentage coverage is important to recognize, but must also be considered in conjunction with the stability of absolute range. A species with a contraction of range and loss of protection should be considered more at risk.	The shift of range may result in a species dispersing to areas where they are protected thus increasing their percentage of protection. Alternatively the shift of range may have no effect if it remains outside of the PAN.

Table 5-16: The relationship between relative protection and change in range due to contraction, expansion, or shift. The conclusions are affected by the current level of protection provided by the PAN.

Table 5-16 demonstrates how a change in a species' range may affect the proportion of that range which is protected, assuming a static PAN. It is possible that a contraction in range can result in better coverage of a species' range by PAs, potentially sending mixed conservation messages. It is therefore important to consider how changes in distribution affect both the

absolute range and the proportion of range that is protected. This is vital when trying to draw conclusions from the results. In general, a small absolute range, large contraction in range, or low percentage of range that is protected are all causes for concern. The evaluation of the protection coverage for a species should therefore incorporate three variables (see Figure 5-22). The three variables may be independently evaluated or combined when considering the protection requirements for a species. While very low absolute range would elevate the need for greater percentage of protected range, if its absolute range is expanding rapidly and already has a high percentage coverage, then other species may demand more attention. As implied above, a large contraction of range and/or small absolute range may render a species a priority even if it has high coverage by protected areas. Equally, very high protection coverage may reduce a species' conservation priority otherwise dictated by range contraction. This is providing the absolute range does not fall to within the threat level categories. With conservation funding finite, such distinctions are necessary to focus on the species most in need.

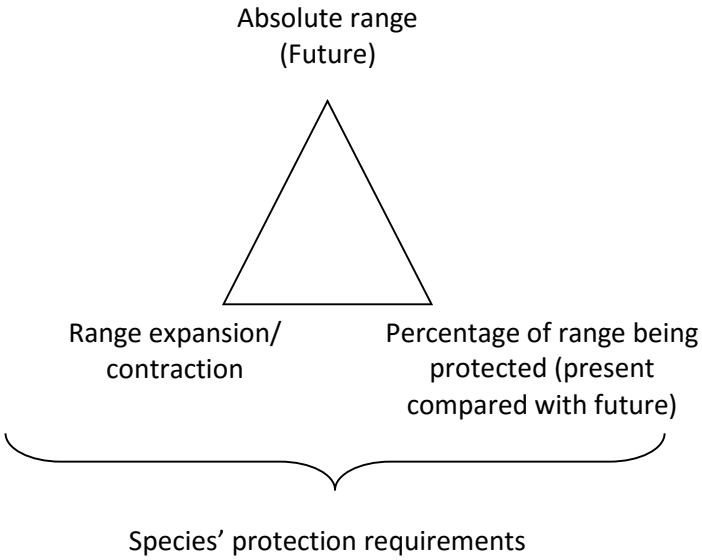

Figure 5-22: Evaluation of the protection coverage provided to a species range should incorporate 3 variables. Each may elevate or reduce concern for that species.

Creating targets and guidelines for the level of protection required for species is a complex task. Only by incorporating each of the variables in Figure 5-22, and understanding the cause of change to those variables, will it be possible to make informed decisions as to the level of PAN coverage required for each species. With so many species to consider, a simpler approach might be to set one target for all. While there are no fixed guidelines as to how much of a species' range need be protected to adequately conserve those species, under the

CBD Aichi targets (Target 11) an aim of 17% of terrestrial areas should be conserved by 2020 (CBD, 2010). Therefore this might be considered the target for species as well. Table 5-15 shows that, given no expansion to the PAN, on average the PAN protects 21.39% of a species range under the pessimistic approach, 17.01% under the envelope. Therefore, if 17% were the target, on average, species are being adequately protected, but large variances exist and many species are not protected to that level. It is prudent to consider the absolute number of species given adequate protection along with the average species coverage. Thirty-three (pessimistic approach) to 40 (envelope approach) species ranges do not have greater than 17% protection if all existing PAs are considered. If, as with the Marxan analysis only IUCN PAs are considered, the numbers of adequately protected species are four and six for the envelope and pessimistic approaches respectively.

Whether the Aichi 17% target is sufficient to protect biodiversity, and the services based on them, is still under debate with some thinking the value should be much higher (Larsen *et al.*, 2014). It is also unclear how setting a blanket 17% of land area (Aichi Target 11) can coexist with Aichi Target 12 which requires that 'By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained'. If threatened species are broadly distributed, the 17% land areas requirement may not accommodate all species (Rodrigues *et al.*, 2004b). The Aichi targets also emphasize the protection of endangered species rather than preserving all species. This is despite the current conservation focus being to emphasize ecosystems/ecosystem services that require a wider spectrum of biodiversity to function. Such an approach may lead to the unthreatened being under-protected and over-exploited, while the status of the endangered remains static, yet achieving the set goals. For this reason, a flat 17% land mass protection seems a political figure rather than a functional one if we are to protect adequately terrestrial biodiversity (see Larsen, *et al*., 2014; Rodrigues, *et al.,* 2004b;). Obviously the 17% Aichi target is not meant to be a realistic target at a species level, and was adopted here to identify areas of relatively high priority and to compare to the LP and HP scenarios presented. However, the associated complications can be illustrated by the dorcas gazelle and the Nile lechwe, a wide and a narrow ranged species respectively (2080 distribution from Table 5-5). The dorcas gazelle, with a potential range of over a third of Africa, would require approximately 6% of the African land mass be protected for that species alone. This 6% would be required in largely arid areas which would be neither logistically nor economically viable to protect. Compounding this problem is the fact that the dorcas gazelle is often the only antelope species present in northern Africa. This reduces

the conservation value of each area, compared to areas that may protect multiple species, or highly restricted species. The contrast with limited range species, such as the Nile lechwe, is vital when developing a PAN to protect all species. The Nile lechwe, forecast to be present in 14 cells in 2080, would therefore require only two cells protection under the 17% rule. This may be insufficient to protect a minimum viable population, or to allow natural behaviour (Mandujano & González-Zamora, 2009; Gaston *et al.*, 2008). It would likely also reduce the opportunity for multiple sites protecting against disease or stochastic events (see Shafer, 2001; Diamond, 1976). This was the reason for implementing the minimum protection limit of 20,000km^2, and the range dependent protection requirements.

There are additional factors, beyond the scope of the study here, that also need to be considered when evaluating the level of protection to be afforded each species such as:

- What other threats face each species (exploitation, competition, predators, disease, genetic diversity, habitat loss)?
- What is the population density of species? This study considered the presence/absence of a species due the limited density data available for most areas and species. However, where species are found to be wide ranging, but in low density such as desert species, these species may require greater protection coverage (Belbachir *et al.*, 2015).
- What is the current estimated population?

All other threats need to be considered when setting goals for percentage coverage, and location of coverage (see Figure 5-23). For example, species threatened with ongoing disease problems may dictate a fragmented approach to their protection to reduce risk. Conversely, those with low genetic diversity may benefit from larger areas with increased corridors to increase gene flow. Species under threat from exploitation may need to be protected in areas further removed from humans or areas of high human density. These factors need to be considered on a species by species basis in conjunction with the type of analysis performed here.

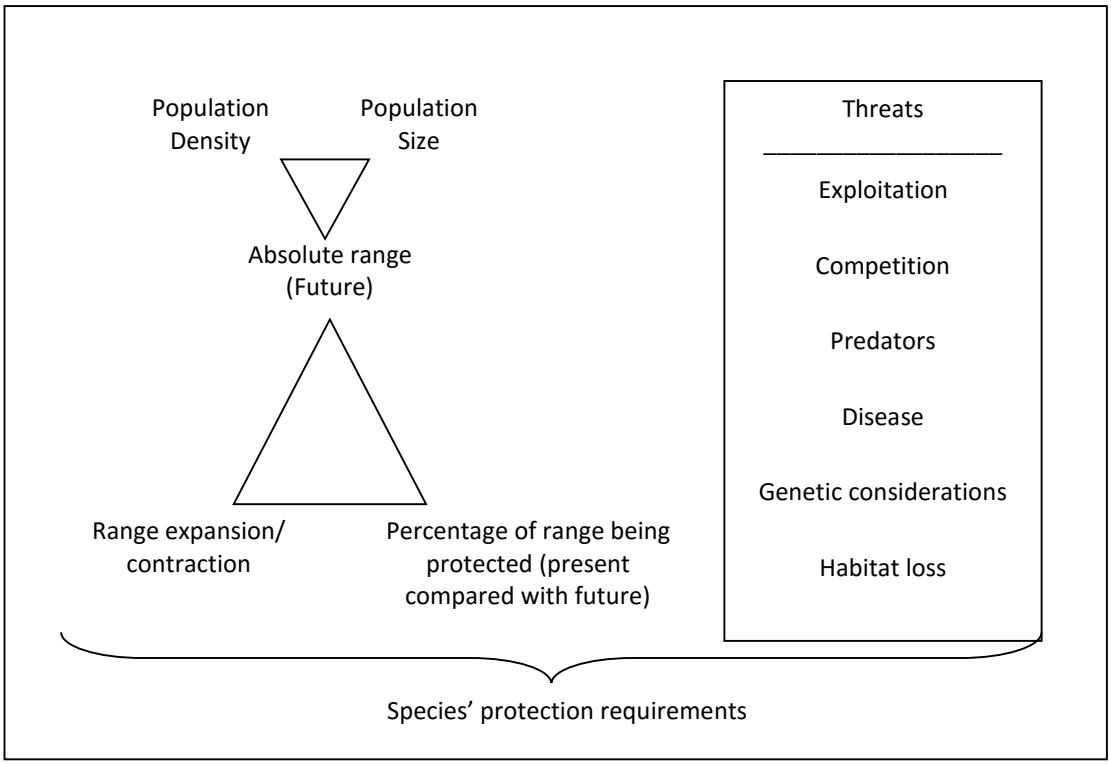

Figure 5-23: Expanding Figure 5-22, additional considerations to be included when evaluating how to determine future range

Limitations of PAN analysis and potential for future improvement

Below I identify a number of areas where future studies may be able to improve on the methods used above if access to further data becomes available.

Costs

The PAN solutions are based on the data, rules, and assumptions provided. The first assumption was that there are infinite financial resources available for the development of the PAN. This was necessary due to the second assumption that the cost of each land unit (grid cell) was equal. This second assumption was required as land value/cost data is not available at this scale. The solutions present optimal PAN recommendations based on those assumptions, the rules provided, and the projected species ranges. The PAN solutions here present a starting point for further discussion and analysis when developing a strategy for the protection of antelopes. As discussed above, this analysis focuses on one group of species whereas a continental conservation strategy would require input from many similar studies on other taxa.

In the future it may be possible to enhance the PAN solutions. Data on the cost of land units would be highly beneficial, as would the inclusion of other rules to include/exclude certain areas. For example, key areas could be included that are important for migration/dispersal

(e.g. Caprivi Strip), or areas of highest diversity for nature tourism purposes (e.g. central Tanzania). Areas to be excluded could be linked to conflict, or war, where enforcing conservation would be unfeasible (e.g. Somalia). All of these could be achieved by altering the value of the cells or by 'locking' those cells in or out of the final solution.

Ultimately, the function of conservation planning software such as Marxan is to establish the most efficient, cost-effective solution for a PAN that protects all species to prescribed levels. These solutions then provide one part of the decision making process when developing a PAN (Knight *et al.*, 2009). However, these solutions ignore the distribution of responsibility. Countries such as Tanzania have very high responsibility (i.e. high PA requirement), due to the overall high levels of species diversity, or endemism, while others will have less despite their similar size, such as Namibia. However, is the burden of funding equally biased? Countries with large PANs may benefit from additional wildlife tourism providing the areas are accessible and the infrastructure is in place to service them, but the initial set-up costs would need to be met by some means. In addition to this, there is a potential threat to the existing PAs that are outside of the PAN solutions created by conservation planning software. If government funding is directed towards those areas within agreed PAN solutions, this could negatively affect other PAs. PAs aim to effectively protect all species within their borders, as well as providing revenue and taxes for the local and national economies. The additional PAs must therefore be recognized for the economic and conservation services they provide, even if priorities are identified to lie elsewhere.

Political constraints

There are additional concerns when producing PAN solutions at a continental scale. International boundaries are ignored, as are areas of human conflict which would render conservation unfeasible. The need for transfrontier parks was demonstrated in Kenya, Namibia, and Tanzania, but such areas would be needed across Africa. To establish solutions based at continental scale requires agreement from each of the African states and a common accord on conservation.

Areas of conflict particularly affect beira, Speke's gazelle, dibatag and silver dik-dik that are found predominately in Somalia (IUCN, 2011). Pessimistic future predictions indicate a contraction of habitat for these species within Somalia and no PA protection is currently provided. Somalia continues to be an area of human conflict and the threat of terrorism within the country remains high (UK Foreign Office, 2014) limiting the potential for conservation efforts within the country. Alternative strategies may need to be considered

to establish protected populations of such species via *ex-situ* conservation in zoos, or via assisted colonization/migration. This is discussed further in chapter six.

Density

The predictions and PAN solutions presented here are based on presence/absence of species in any cell and do not take population size or density into account. The rules in place define levels of habitat to be protected rather than a specific population size. The data on species density are not available for most species at the levels required to produce population models and forecasts at a continental scale. While species density may vary due to disease, climate, competition, predation, habitat suitability, food supply, space (Owen-Smith, 2002; Osbourne, 2000; Solomon, 1949; Whittaker, 1975), or exploitation, there are general rules that apply. For example, desert/arid adapted species are typically found at low density due to fewer resources (Mésochina *et al.*, 2003). Therefore it may be that small ranged, arid adapted species require proportionally larger areas of their habitat protected compared with species that inhabit resource-rich areas.

Scale

The cells with PAs described here do not necessarily protect the whole cell. The central point determinacy method of obtaining whether the PA is present (see 2.1) has its limitations. Conversely, however, there are cells that have protected areas that would not be recognized using the methodology applied. An optimal solution would be to use a far finer scale. This would require the original climate data to be processed at a finer scale such as 0.5'. While this data is available, the downscaled nature of the data means that it is no more valid than the scale used above. This would also extend processing time by approximately 400 times. It is suggested that, at a continental scale, the methodology used herein is suitable for the task.

Database design

In 2002 the World Database of Protected Areas (WDPA) was established to provide an up-to-date, accurate database of global PAs. This database was for conservation professionals, and others, to aid in the analysis of existing conservation provision and future planning (Rodrigues *et al.*, 2003).

The data held in the WDPA needs to be refined. The database itself needs to enforce the entry of valid data via database rules. Many of the fields are freeform text that leads to difficulty in analysing data or grouping that data. An example of this is the country field,

normally a simple three letter code, this can include multiple countries for trans-boundary reserves. However, some users have misunderstood this and added entries such as "AGO, AGO" where multiple sub-locations exist within one country. This is not the correct use for this field. The database allows the use of multiple countries in one field, for example "TZA, KEN". This is an unusual database design. Databases are specifically designed to be able to handle data such as these one-to-many relationships. Trans-boundary reserves should have multiple records designating each country (see Figure 5-24). For this study, this only affected the country specific identification of protected areas, and these were managed on a case by case basis and placed into the relevant country based on actual location. There are also inconsistencies as to where information is entered. An example of this is the community data where users had used three fields to indicate community conservation areas. This was identified and all PAs were divided into the three categories (IUCN, community, and supplementary).

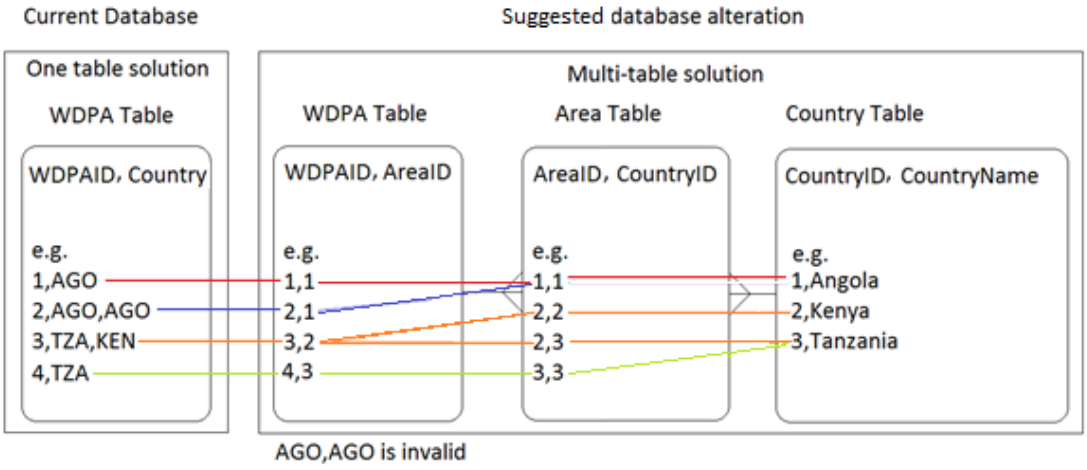

Figure 5-24: Suggested database alteration to accommodate trans-boundary protected areas. The use of multiple tables allows end-users to simply query the database by country where the existing one table solution requires a more complex approach. In this example, row three ('TZA, KEN' in current database) has 1 WDPAID, linked to 2 areas (area IDs), that are linked to country codes (Yellow link lines).

Further concern for the data quality in the WDPA is found in core fields within the database. For example, in Africa alone the WDPA lists 134 types of PA (PA designations), including the sub-separation of seven IUCN categories. There is significant overlap in these designations across countries, but with slightly revised naming conventions. This highlights a lack of coordination, clear distinction, and understanding of PAs' designations and management objectives. Furthermore, many database fields are not completed and classified "Not Reported" for many of the records. This is allowed by the metadata definition, and did not affect this study. However, considering the importance of these data it is suggested that

most of the fields be listed as required with a limited set of options for those fields to enable efficient analysis.

Conclusion

This study highlights the importance of considering multiple factors and variables when prioritising species for protection, and setting protection targets. The hirola, already considered one of the most highly threatened antelope in Africa (IUCN SSC Antelope Specialist Group, 2008a), is predicted to have no suitable climatic conditions in the future and is therefore high in terms of conservation concern. However, the story is more complicated for other species. Species may have relatively high levels of protection predicted in the future, but this may be a result of relatively small range (e.g. mountain nyala) and/or a rapidly contracting range (e.g. Nile lechwe). Other species have relatively large ranges, but have no protection as they occur in politically unsettled areas (e.g. dibatag, Speke's gazelle, and beira). Only with access to, and understanding of, all of these data is it possible to begin to build a cohesive protection plan for all species. The results and PAN solutions above provide the opportunity to study these and other individual species, identify those most threatened, and provide suitable areas of protection for them in the future.

The future looks bleak for the hirola with no suitable conditions indicated, however, this does not mean that there are no climatically suitable areas in Africa. The methods used above restrict areas considered as suitable to those connected to the species' existing range; this is to better understand the potential of species to persist given barriers to dispersal. Acceptable climatic conditions may however be available elsewhere, but remain inaccessible over the next century. For threatened antelopes such as the hirola, natural dispersal to these areas may be restricted either by distance or due to human activities, and in these cases, alternative strategies may be required such as assisted migration or colonization, whereby a viable population may be translocated to a more remote area. Assisted migration brings ethical and scientific questions (McLauchlan *et al.*, 2007) that are considered, along with specific options for the most threatened species, in chapter six.

6. Using predictive species distribution modelling to prioritize opportunities for translocation under climate change

Abstract

Climate change is resulting in species altering their distributions (Parmesan, 2006). Through dispersal this spatial response to climate change enables some species to track suitable climatic conditions. However, multiple threats impact species distributions and populations globally. For Africa's antelopes, human exploitation, disease, agriculture, and habitat loss all contribute to range loss, reduced populations, and a threat status for 26% of species (IUCN, 2014a). A quadrupling of the human population in Africa by 2100 (UN, 2014) is likely to place increased pressure on existing antelope populations resulting in restricted dispersal. Furthermore existing fences around protected areas and between countries, originally erected to protect these populations, could also restrict dispersal.

In this study 14 species are identified as having a threat status assigned due to climate change based on IUCN criteria or are considered threatened here due to having no protected area coverage within their predicted range at the end of 2080. Based on predicted species distributions under the A1B climate scenario, the hirola (*Beatragus hunteri*) and Aders' duiker (*Cephalophus adersi*) are predicted to have no suitable climatic conditions within or connected to their existing range. However, for all species climatically suitable conditions are present in Africa and protected areas are found within those regions.

Finally, I also present analysis of potential competition based on novel antelope species encountered and niche overlap within suitable areas. If species are unable to naturally disperse, this analysis will help to identify areas for translocation projects. I also review the need to address existing translocation terminology. Currently, species translocations performed outside of indigenous areas (assisted colonization) are considered a greater risk than those conducted within the historic range (assisted migration). However, changing climatic conditions naturally alter species indigenous range if they are able to disperse. I therefore suggest that translocations of animals to areas of predicted suitable climatic conditions where species are unable to disperse due to human pressure, be considered 'assisted dispersal' to 'projected indigenous' areas.

Introduction

Climate change (CC) is a leading concern for conservation professionals requiring a cohesive worldwide response. Despite targets being set, such as limiting warming to 2°C above pre-industrial levels, temperatures continue to increase beyond the worst case scenario (Peters *et al.*, 2013). While there is an inevitable background rate of extinction driven by natural events and processes, extinctions caused by anthropogenic CC should be prevented where possible. Every species has a bioclimatic envelope that defines the climatically suitable conditions where species may be present (Araújo & Peterson, 2012). Conditions within a species' existing range may be pushed outside of that envelope by CC (Hannah *et al.*, 2005; Thomas *et al.*, 2004). Species have a number of possible responses to CC including (a) spatial changes where species disperse to more favourable conditions and habitat; (b) temporal changes altering phenology; and (c) evolutionary changes (Bellard *et al.* 2012). Failing these responses extinction faces species. To date, most responses displayed by species have been spatial range changes (Thomas, 2010; Hickling *et al.*, 2006). Spatial changes rely on a species having suitable habitat to move into and not being limited by geographic, ecological, or human barriers. They must also be able to disperse in time with CC conditions, and for there to be suitable climatic conditions available. Each species' bioclimatic envelope can result from a complex combination of interrelated requirements linked to ecological and morphological traits (see chapter three). Changes in climates are also complex and do not always shift suitable conditions from one area to a neighbouring area, and this may prevent the possibility for dispersal (see chapter four). Suitable conditions may be present, but unreachable leading to the need for translocation of those species if they are to survive.

Declines in population, and even more so the extinction of a species, reduce genetic diversity and can have wide ranging ramifications for humans and ecosystems (Sodhi *et al.*, 2009). A single species' extinction can affect humans directly through loss of food, fuel, and medicinal sources. It may also affect humans indirectly through trophic interactions and ecosystem service collapse. Further to this there are the cultural, aesthetic, spiritual, and economic benefits that may be lost (Chapin III *et al.*, 2000). The need to further understand which species are likely to be threatened by CC, and then how to mitigate or eliminate those losses, has never been greater. Here, focusing on African antelopes I identify species that are (a) threatened specifically by CC based on the IUCN criteria, and/or (b) at risk due to lack of protection. I then assess opportunities for translocation of those species. This diverse group of animals highlight many of the costs associated with biodiversity loss. Antelopes play vital

ecological roles as prey, contribute to nutrient cycling (McNaughton & Georgiadis, 1986) and seed dispersal (Feer, 1995), and are habitat architects (Bond, 2008; Augustine & McNaughton, 2004; Prins & van der Jeugd, 1993). They provide a vital source of protein to indigenous populations throughout Africa and contribute to local and national economies through tourism. Africa's human population is predicted to rise from 1 billion to 4 billion by the end of the century (United Nations, 2014). This seems likely to place added pressure on antelope populations as a source of human food.

The IUCN currently lists 19 African antelope species as threatened. The threats include habitat loss and agricultural encroachment linked with disease, over-exploitation through hunting, and climate change (largely related to drought and habitat-loss caused by desertification). Also highlighted, although not directly as a threat, is the lack of protected area coverage for species such as the dibatag (IUCN, 2014a). While CC is listed as an existing threat, it is unusual for CC to be used in the justification for antelope being categorized as threatened (vulnerable, endangered or critically endangered), although three of the arid adapted species are listed as threatened by drought. This is likely related to the fact that all threat justification for African antelope species relates to a decline in population in the past (three generations) or absolute population/location numbers. Antelopes are not alone in having CC listed as a threat for so few species. Akçakaya *et al*. (2014) found that only 10.5% of species listed as threatened included "climate change and severe weather" as a threat. This suggests a mismatch with the many studies that suggest threats to a wide range of species (Foden *et al.*, 2013; Thomas, 2010; Hickling *et al.* 2006; Thuiller *et al.,* 2006a, 2006b; Hannah *et al*., 2005).

The IUCN has provision for a species to be declared threatened via a wide range of criteria including projections. Here, using ensemble projections of antelope species distributions for 2080, two IUCN criteria that can be assessed by projections are used to establish threat status. The IUCN B2 criterion assesses a species' area of occupancy (AOO) whereby an AOO under 2,000km^2 places the species in the vulnerable category or worse. The IUCN A3 criteria assesses population decline over three generations or ten years, whichever is longer up to 100 years; for all African antelope species this corresponds to three generations. Under this criterion a species declining in population by 30% over three generations is deemed vulnerable or worse. CC projections often work on timeframes which are longer than three generations. Here the time frame is considered to be 80 years and the decline in distribution over three generations is calculated from that. In addition, species projected to have no

future range are considered threatened under both A3 and B2. Finally, species not found in any IUCN protected areas are considered threatened for the purposes of this study.

To identify species at risk, the ensemble projections used to assess each species' future range assume a pessimistic view of the future where a species cannot disperse from its current range. This is suggestive of a future where species are increasingly under pressure from humans. However, the projections provide further areas that are climatically suitable outside their current range. These areas can be separated into two categories: (a) those that are connected to the existing range over the next 80 years (connected areas); (b) those that have no connection to the existing range (unconnected areas). Connected areas are indicative of areas which a species could reach if unaffected by humans and dispersal barriers other than spatial gaps. Unconnected areas are climatically suitable but would not be reached through natural dispersal. If a species is limited to its current range, the connected and unconnected areas present opportunities for translocation to found new populations for species at risk. However, such translocations highlight ethical and scientific questions that should be addressed on a species by species basis.

The terminology relating to translocations is complex and depends on the location and reason for that movement of animals. 'Translocation' refers to the human movement of individuals from one area to another. Here, translocation is used as an abbreviation for 'Conservation translocation' which is defined by the movement being for a conservation purpose (IUCN/SSC, 2013). This encompasses a number of sub-categories (derived from the IUCN definitions):

- Population restoration: the release of individuals within that species' indigenous range where that range is defined by the known or inferred historic distribution of the species. This is further split into:
    - Reinforcement: supplementing an existing population with external individuals
    - Reintroduction: repopulating an area where that species was previously extirpated
- Conservation introduction: the release of individuals to areas outside of that species' indigenous range and further divided as:
    - Assisted colonization: introduction of individuals of a new species, outside of their indigenous range, to avoid the extinction of populations of that focal species (synonyms: assisted migration, managed relocation)

- Ecological replacement: to introduce a species to perform a specific ecological function.

Under these definitions any translocation to an area outside of the species' existing range is considered an introduction unless historic range could be identified. According to this terminology a species' existing distribution is considered as its indigenous range. All climatically suitable areas outside of the indigenous range in the future are considered non-indigenous. Any translocation to these areas is a conservation introduction and would be categorized as an assisted colonization. However, here I consider translocations to future climatically suitable areas under a new category called "projected indigenous" if that species is predicted to be able to disperse to those areas naturally. Therefore, for the purposes of this study I define a new category of translocations: whereas any translocations to 'unconnected' areas are considered "assisted migration" or "assisted colonization" (AC) in line with the IUCN definitions, translocations to projected indigenous areas are termed "assisted dispersal" (AD). AC and AD are options for conservationists to either protect them in other areas beyond natural dispersal range or assist species to disperse. Other options include the establishment of habitat corridors to assist dispersal, and increasing suitable habitat near existing ranges (Hewitt *et al.*, 2011). However, given the uncertainty about such initiatives, and in accordance with the precautionary principle, here the assumption is that species are unable to disperse and AC or AD are the only options available.

The merits and drawbacks of translocations, both reintroductions and assisted colonizations, have been questioned for decades. Assisted colonizations particularly should be considered carefully due to the ecological, social, and economic risks they can cause (IUCN/SSC, 2013; Hewitt *et al.*, 2011; Mueller & Helmann, 2008; McLauchlan *et al.*, 2007). The threats from invasive species are varied and all contribute to adverse ecosystem impacts. Concerns include genetic dilution through hybridization (Ricciardi & Simberloff, 2009), the division of conservation resources, and the bias towards individual species (Hagerman *et al.*, 2010). On the opposing side of the debate come those that highlight the prevention of biodiversity loss (for poor dispersers and where habitat fragmentation limits dispersal), benefits for genetic fitness and ecosystem services, and advances in conservation science (Hewitt *et al.*, 2011). As the debate continues, a majority of experts (20 of 21) have stated that interventions are already "central to conservation" and "increasingly necessary". Despite this, there was a general reluctance expressed towards the idea of assisted migrations. Still, most also acknowledged that they would be necessary in some cases (Hagerman *et al.*, 2010).

Evidence that translocations can be successful for antelope species largely comes from reintroduction efforts. In Africa and the Middle East seven arid adapted species have been the subject of reintroduction efforts (Stanley Price, in press). In Africa the reintroductions of addax, dama gazelle, dorcas gazelle, and scimitar horned-oryx remain within fenced areas. The success of each species is variable with dorcas gazelle thriving while the dama gazelle is not. This may be linked with a lack of ecological and behavioural knowledge regarding dama gazelle (Stanley Price, in press) and highlights the need for careful consideration of each species' needs. Also highlighted is the need for good security. In the Middle East Arabian oryx (*Oryx leucoryx*), mountain gazelle (*Gazella gazella*) and sand gazelle (*Gazella leptoceros*) have populations in unfenced areas that vary in success. However, the opportunity for success is demonstrated by the Arabian oryx having been downlisted by the IUCN from 'Extinct in the Wild' to 'Vulnerable' due to multiple reintroduced populations covering six countries (Stanley Price, in press).

The reintroduction success referred to above gives cause for cautious optimism, but it is important to recognize that many of these examples relate to arid-adapted species. Arid areas are less species-rich (Olff *et al.*, 2002) with fewer interspecific relationships to consider and less complex trophic interactions than in less arid environments (Polis, 1991). Potentially these factors could contribute to greater reintroduction success compared with more complex environments. The African reintroduction examples above also relate to groups of animals that have been released into, and remain in, fenced areas with careful management. The success of the reintroductions has broadly been measured by the increase or decrease of the reintroduced species' population size, rather than acknowledging wider ecosystem function or impact on other species. Not acknowledging or assessing the wider impacts might imply success when damage is being caused elsewhere. Incorporated in this study are species with a wide spectrum of ecological and climatic needs, thus including areas where antelope species diversity is greater than seen in arid areas. Both AC and AD involve introducing species into novel areas. This could give rise to interspecific competition with novel species having negative effects (IUCN/SSC, 2013). In this chapter I highlight areas where novel species, i.e. antelope species in the predicted future range which are not present in a species' existing range, would be encountered and interspecific niche overlap is a concern. Specifically, reintroductions into arid areas may be simpler because there are fewer other species to consider.

IUCN guidelines on selecting translocation release sites make no reference to the area having adequate protection (IUCN/SSC, 2013). Although this may be implied, the need for sustained protection of reintroduced animals, particularly from poaching, is required to ensure success (Grey-Ross *et al.*, 2009; Dunham, 2001; Spalton *et al.*, 1999). Any translocation would therefore likely require the release area to be part of a protected area to ensure that the human threats are minimized. For this reason the protected areas with an IUCN management category (Ia to VI) are offered particular attention in this chapter. Other protected areas are present in Africa, as is the opportunity to develop new sites specifically for any translocation project, however, the IUCN sites are assumed to indicate areas with established longer term management.

All of these considerations must be addressed when planning conservation strategy for the future. Here I aim to provide options and information for making informed decisions when selecting species and potential areas for intervention via AC or AD. In this chapter, I focus on potential translocation areas under climate change for the species at risk under the pessimistic approach according to the abovementioned criteria.

Methodology

All statistical analyses were carried out using *R* v. 2.15.2 (R Core Team , 2012). The future range suitability is predicted using the r BIOMOD package (Thuiller *et al.*, 2009) which is then limited using the connectivity methodology (see 2.8). Species current range data is based on the IUCN distributions (IUCN, 2011) rasterized to 10' grid cells (hereafter cells) (see 2.1).

Species future range data is based on projections under the A1B climate scenario ensemble models produced in chapter four for both the pessimistic and envelope modelling approaches. The rationale for use of A1B climate scenario is that it is considered a balanced scenario offering a future between A2 and B1. Quadratic generalized linear models, using climatic variables (see chapter three), predict the suitable areas for each species at 2030, 2055, and 2080. Here I use three categories of climatically suitable area (range types) for 2080 based on the following definitions and assumptions (see also Figure 6-1):

1. The core range. This is based on the pessimistic approach (see chapter four) where species are unable to disperse. It therefore takes the climatically suitable area in 2080 as a subset of the current IUCN distribution. This represents a future where

dispersal is limited by humans. The pink area on Figure 6-1 shows the limit of the core range, i.e. the current IUCN distribution for addax. In this example addax has no suitable climatic conditions within this area in 2080 and would therefore have no core range.

2. The connected range. This is based on the envelope approach (see chapter four) that provides the current and future range for a species based on suitable climatic conditions for each species. This approach requires that suitable areas must be connected to the current IUCN distribution over time. Therefore the future range must be connected to the previous time periods range (i.e. present to 2030 to 2055 to 2080). No limit is placed on dispersal. The blue area on Figure 6-1 shows the connected range. In this example the blue cells have lost their connection to the IUCN distribution (present to 2080), but they have been connected over time. Therefore, if unhindered by humans and dispersal ability, the species would have the potential to populate these areas.
3. The unconnected range. The unconnected range consists of areas that are climatically suitable in 2080, but not connected to the existing IUCN distribution through time. This can establish remote areas that are climatically suitable but unreachable. This is based on the envelope approach, but without the restrictions of being connected to the current IUCN distribution. The green area on Figure 6-1 shows the unconnected range.

Each of these range types consists of a number of cells of that type (i.e. the core range consists of core cells). These range types allows assessment of a species' future climatically suitable range, and protection via IUCN protected areas (PAs) within those given ranges.

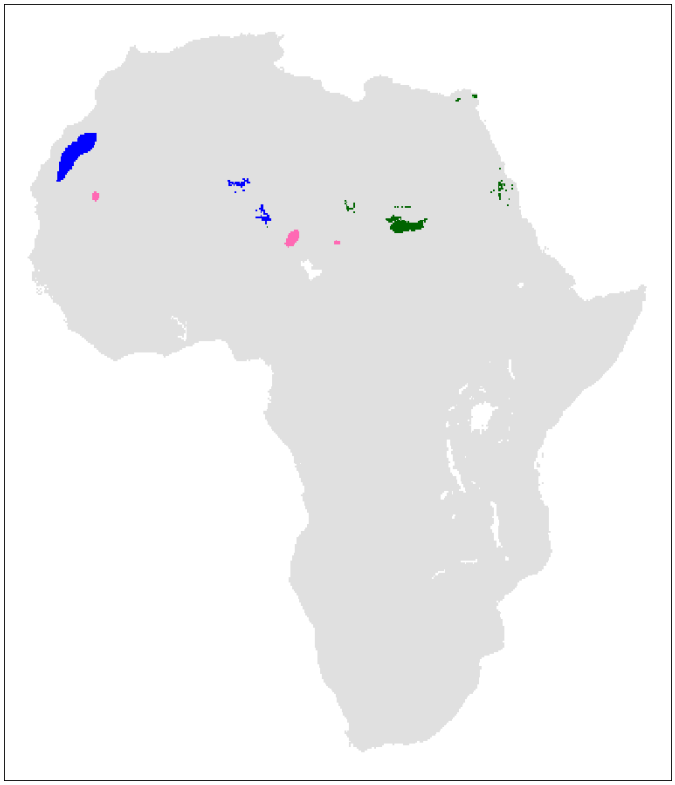

*Figure 6-1: Core, connected and unconnected ranges for the addax (*Addax nasomaculatus*). Pink represents the current IUCN distribution and the limit of the core range (this is completely lost for the addax): Blue denotes the connected range based on the envelope approach; the connected originated from the IUCN distribution but over three periods has become disconnected and fragmented, however, it is considered connected due to its origin. Green is the unconnected range; these areas are climatically suitable in the future (2080 period) but have not been connected to the IUCN distribution over time.*

A habitat filter is applied where species may be assigned to open or closed habitat types according to their specialist foraging preferences (see 2.7). Thus, species may be restricted to open (grassland/savannah) or closed (dense woodland/forest) areas, or be generalists that can move freely. This limits the connectivity under the envelope approach and restricts areas from being suitable under all methods.

I extend and modify the existing definitions found in the IUCN translocation guidelines (IUCN/SSC, 2013) as follows. The classifications "projected indigenous" and "assisted dispersal" were added as divisions of the existing non-indigenous and assisted colonization classifications respectively (see Table 6-1).

Grouping	Classification	Definition
Distribution or range	Indigenous	Current range of the species. Used as a starting position for the pessimistic approach.
	Projected indigenous	Projected to be climatically suitable and connected to the existing distribution over time. Connected areas identified using the envelope approach.
	Non-indigenous	Projected to be climatically suitable but unconnected to the existing distribution. Areas identified as unconnected areas.
Translocation type	Reintroduction	Translocation to indigenous area
	Assisted dispersal (AD)	Translocation to projected indigenous area
	Assisted colonization (AC)	Translocation to non-indigenous area

Table 6-1: Classification used in this study. These are modified and extended from the IUCN translocation guidelines (IUCN/SSC, 2013).

Species selection and threatened status

In this section I describe the IUCN definitions for assigning threat status in greater detail and how they are applied in this chapter. The species selected for this study include those where their threatened status is directly attributable to the effects of CC under the pessimistic approach and those whose future range includes no IUCN protected areas. Hence, the aim is to identify all species that are threatened by climate change, or through a lack of protection, irrespective of their existing threat status. The species threat statuses are assigned based on the IUCN categories (described below) under the following criteria: (i) species predicted to have no suitable range in 2080 (IUCN criteria A3 and B2); (ii) species that have an elevated threat status based on a reduced area of occupancy (IUCN criteria B2) between now and 2080; and (iii) species that have an assigned threat status based on a projected population decline (IUCN criteria A3).

The IUCN definitions are typically used to assess the threatened status of a species (IUCN Standards and Petitions Working Group, 2008). There are a number of categories under which a species can be deemed threatened. Under these categories a species' threat status level increases in severity as follows: levels least concern (LC), near threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW), and extinct (EX). Not all criteria apply to the impact of future climate change (Akçakaya *et al.*, 2006); however, the following lend themselves for assessing species range or area of occupancy (AOO). Criteria B1 and B2 give provision for a species to be classed as VU if the

extent of occurrence (EOO) is less than 20,000 km^2 (B1), or where AOO is less than 2,000km^2 (B2). Species are further classed as EN and CR if their EOO falls to less than 5,000km^2 and 100km^2 respectively (B1), or AOO falls to less than 500km^2 and 10km^2 respectively (B2). This EOO equates to less than 59 cells, where each cell is ≈344km^2 at the equator (20,296km^2). EOO and AOO are distinct, the former is based on the production of a minimum convex polygon around the species' known locations whereas AOO is the sum of the cells where the species is present. However, the EOO minimum convex polygon can be split into multiple areas where the areas between are "obviously unsuitable habitat" (IUCN, 2012). The original models that define each species' presence or absence in a cell, are based on IUCN spatial data. These distributions, presented as polygons, contain the known, inferred, or projected range of each species, these may be split into multiple areas (IUCN, 2011). These are better described as AOO rather than EOO data as the polygons are closely tied to the species ranges and not minimum convex polygons. They can also include islands within the polygons where the species is not present. Therefore, the rasterization of the IUCN distributions creates an AOO representation of a species' range based on the IUCN acceptance of inferred and projected range. The projected distributions are thus the predicted AOO for each species.

When assessing AOO the IUCN requires a maximum scale of 4km^2 compared with the ≈344km^2 used here. Any greater scale does not permit a species to be classified critically endangered as the upper limit is 10km^2 under criteria B2. The IUCN provide scaling down methodology (IUCN Standards and Petitions Subcommittee, 2014) which was used to produce AOO estimates at 4km^2 resolution. This uses the cartographic method of doubling grid dimensions requiring the conversion of the existing ≈344km^2 data to a coarser ≈1,376km^2 before scaling down based on Kunin (1998) and He & Gaston (2000) (see Equation 6-1; see IUCN Standards and Petitions Subcommittee, 2014 for workings). Table 6-4 shows all species considered in this study highlighting those whose future ranges are under the 2,000km^2 threshold.

$$A_a = A_{a2}\left(\frac{a}{a2}\right)\frac{\ln A_{a2} - \ln A_{a1}}{\ln a2 - \ln a1}$$

Equation 6-1: Kunin's (1998) "area-area curve" (see He & Gaston, 2000) used in the IUCN scale down methodology (IUCN Standards and Petitions Subcommittee, 2014) where A_a is the occupied area at fine-scale a. A_{a1} and A_{a2} are the total occupied area at two coarse scale grids where the minimum map unit (map scale) is $a1$ and $a2$ respectively.

Scaling down methods can prove unreliable given different species dispersal ability, habitat specificity, etc. (IUCN Standards and Petitions Subcommittee, 2014). However, with limited options available to assess future species ranges, the above proves a valuable tool for

estimating species threat status. For the purposes of this study, an AOO, and the threat status associated with that value, is calculated for each species' range at present and in 2080. If the threat status increases then the species was included in the study.

IUCN criteria A3 defines threatened status based on a "population size reduction of 80%, projected or suspected to be met within the next 10 years or three generations, whichever is longer" where 80% represented the CR threshold and is replaced by 50/30% for EN/VU respectively (IUCN Standards and Petitions Working Group, 2008). This 'reduction' may be based on the AOO or EOO for the species (A3c). The IUCN bases this calculation on three generations, but when considering climate change the periods contemplated are longer. For this reason an extrapolation is used to find a population (number of cells a species is present) reduction threshold over an 80 year period (2010-2090) where a rolling reduction of 30/50/80% takes place every three generations. For example, a species with a population of 100 and a generation length of 6 years would be vulnerable if the AOO reduction was 30% over 18 years leaving a population of 70. The extrapolation then takes a further reduction of 30% over the next three generations (i.e. population 49 after 36 years) and continues until 80 years is complete. For example, for a species with a six year generation time this is 14 generations (84 years). For the final period two generations reductions are subtracted to be greater than or equal to the 80 year period. The 30% reduction is divided by three; therefore twice times 10% population reduction for the final period leaving a population of 19.2. Therefore a species with less than 19.2% of its existing IUCN range (considered 100%) indicates a vulnerable species where that species has a six year generation time (see Table 6-2 for this worked example).

Example species	Dibatag					
Generation length	6					
Period	0	1	2	3	4	5
Generations	0	3	6	9	12	**14 (2 only)**
Years	0	18	36	54	72	**84 (over 80)**
Population reduction	0	30%	30%	30%	30%	**20% (for 2 generations only)**
Population remaining	100	70	49	34.3	24	**19.2 (19.2%)**

Table 6-2: Worked example for calculating a species' multi-generation decline over an 80 year period. A species with a generation of 6 years experiences four full three generation periods and an additional two generation to pass over the 80 year requirement. This incremental population reduction results in a threshold of <19.2% population remaining (or an AOO/EOO reduction to 19.2% of current) to indicate the species is vulnerable.

The generation length, which is defined as the average age of adults in a population (i.e. older than first breeding age; IUCN, 2012) for all antelope species is not available. The IUCN

red list contains generation length values for 12 species (IUCN, 2014a). The adult body mass (natural log) strongly correlates with generation length (p=0.006; r=0.74; n=12) and therefore a linear model provides the generation times for the remaining species (adult body mass source data from Bro-Jørgensen, 2007; Bro-Jørgensen, 2008; Bro-Jørgensen, unpublished; Kingdon, 1997; Estes, 1991). Generation lengths in years were conservatively rounded down to the nearest whole number.

The lack of protection is considered a concern for some species, but is not a criteria used when considering whether a species is threatened. For example, the IUCN justifies the dibatag as vulnerable due to overexploitation, habitat degradation, and competition with livestock. Lack of protection is considered a threat (IUCN SSC Antelope Specialist Group, 2014), but this is not a criteria to establish threat status. Typically such species could be categorized endangered due to a projected population decline however, this is unlikely in areas where no data exists and/or surveys cannot be completed. For this reason I have highlighted those species whose future range did not overlap with any IUCN PAs. PAs data were from the world database of protected areas (United Nations Environment Programme World Conservation Monitoring Centre, 2010) and only IUCN PAs were included in the analysis (see chapter five).

Niche overlap of species

Assisted colonization and dispersal can introduce the focal species (i.e. that species being translocated) to novel species and can therefore potentially introduce increased foraging competition and possibly displacement of indigenous species. To identify areas of concern the number of novel antelope species are identified in each species' future predicted range (both connected and unconnected). In addition Pianka's niche overlap index (Equation 6-2), a measure of niche overlap between two sympatric species (Pianka, 1973), is calculated between the focal species and all sympatric species within each cell. This is then averaged to produce the mean niche overlap. The niche overlap between two species is calculated according to the percentage of fruit, browse, and grass in each species' diet (Gagnon & Chew, 2000; Cerling *et al.*, 2003; see 2.5.3.3 for data sources).

$$O_{kj} = O_{jk} = \frac{\sum_i^n P_{ij} P_{ik}}{\sqrt{\sum_i^n P_{ij^2} \sum_i^n P_{ik^2}}}$$

Equation 6-2: Pianka's (1973) niche overlap index (O) of species (k and j) where P_{ij} and P_{ik} are proportional use of the i^{th} resource by the j^{th} and k^{th} species giving a pairwise species overlap value between 0 (no overlap) and 1 complete overlap.

The mean niche overlap is calculated for each cell of the focal species' current range and averaged to find the niche overlap within the indigenous range. This in turn is used to compare against niche overlap in connected and unconnected areas.

The mean niche overlap used here is modified from the conventionally used method to provide information on niche overlap specifically pertaining to the focal species, i.e. here, the mean niche overlap for a cell is defined as "the mean of the niche overlap values between the focal species and the other species in a grid cell". The conventional method takes the mean of the niche overlap values between all paired species within a cell (Luiselli, 2008; Luiselli, 2006). It should be noted that Pianka's index is not a direct measure of competition, but allows the identification of species that have overlapping resource requirements (Winemiller & Pianka, 1990).

Kruskal-Wallis rank sum tests were used to compare the mean niche overlap of cells across all range types (i.e. current, connected, and unconnected). Pairwise comparisons using Nemenyi post-hoc tests identify significant differences between range types. Non-normal target mean niche overlap data generated using Pianka's index required a non-parametric test. χ^2 and P values are reported for the comparisons between current and connected/unconnected combined, in addition to each pair (i.e. current/connected, current/unconnected, connected/unconnected).

Climate scenario selection

There is uncertainty attached to climate projections with multiple climate scenarios representing futures based on differing levels of global greenhouse emissions, world population growth, and technological advances (IPCC, 2013a; New *et al.*, 2002). The A1B climate scenario used here presents a hopeful, but realistic view of the future where a mix of fossil fuels and renewables are used and where population growth peaks mid-century (IPCC, 2007). Global organizations moreover create different climate models and produce climate projections based on these scenarios, and these climate projections differ between organizations. Here I use species distributions, predicted using projections from three climate models, to create ensemble models. These ensemble models provide greater confidence on suitable areas for each species (see chapter four).

Results

Fourteen species are predicted to be threatened due to climate change or lack of protection (summarized in Table 6-3) based on the following criteria: (i) species predicted to have no suitable range in 2080 (IUCN criteria A3 and B2); (ii) species that have an elevated threat status based on a reduced area of occupancy (IUCN criteria B2) between now and 2080; (iii) species that have an assigned threat status based on a projected population decline (IUCN criteria A3), and (iv) species whose future range includes no IUCN protected areas. Based on the pessimistic approach where species ranges cannot expand beyond their current range, four species (addax, hirola, Aders' duiker, and Nile lechwe) have no core range remaining and face extinction (see Table 6-4). A further five are at risk due to small range (see Table 6-4: dibatag, Abbott's duiker, silver dik-dik, dama gazelle, and mountain nyala). Nine qualify due to a rapidly contracting range (see Table 6-5: addax, dibatag, hirola, Aders' duiker, Peter's duiker, white-bellied duiker [*Cephalophus leucogaster*], Nile lechwe, silver dik-dik, and dama gazelle), and five have no protection (see Table 6-6**:** dibatag, Jentink's duiker, beira, Speke's gazelle, and silver dik-dik).

Criteria	Criteria description	Species affected
Extinction (EX)	The species range is completely lost between present and 2080. This could be considered IUCN criteria B2 or A3.	Addax (*A. nasomaculatus*) Hirola (*B. hunteri*) Aders' duiker (*C. adersi*) Nile lechwe (*K. megaceros*)
No protection (NP)	There is no IUCN protected areas protection for the species in their future range. Other protected areas are assumed to provide unreliable long term protection.	Dibatag (*A. clarkei*) Jentink's duiker (*C. jentinki*) Beira (*D. megalotis*) Speke's gazelle (*G. spekei*) Silver dik-dik (*M. piacentinii*)
Small range (SR)	The AOO of the species has contracted to <2,000km^2 and the species has an elevated threat status based on IUCN B2 criteria derived from AOO calculations for the present and 2080.	Dibatag (*A. clarkei*) Abbott's duiker (*C. spadix*) Silver dik-dik (*M. piacentinii)* Dama gazelle (*N. dama*) Mountain nyala (*T. buxtoni*)
Projected reduction in population (PRP)	A threat status assigned due to projected population reduction of 80/50/30% over three generations extrapolated to 80 years based on variable generation times (based on IUCN criteria A3).	Addax (*A. nasomaculatus*) Dibatag (*A. clarkei*) Hirola (*B. hunteri*) Aders' duiker (*C. adersi*) Peters' duiker (*C. callipygus)* White-bellied duiker (*C. leucogaster*) Nile lechwe (*K. megaceros*) Silver dik-dik (*M. piacentinii)* Dama gazelle (*N. dama*)

Table 6-3: Species identified as threatened due to climate change based on IUCN and novel criteria.

Species		Period	Number of grid cells the species is present (2080) at grid cell resolution		Area of occupancy at different scales (km²)			Approximation of scale factor (C)	IUCN threat category based on criteria B2
			≈344km²	≈1376km²	≈344km²	≈1376km²	≈4km²		
Addax	*Addax nasomaculatus*	Present	99	35	34,056	48,160	**11,185.1**	0.250	LC
		2080	0	0	0	0	**0.0**		CR/EX
Dibatag	*Ammodorcas clarkei*	Present	245	77	84,280	105,952	**40,400.7**	0.165	LC
		2080	5	4	1,720	5,504	**41.0**	0.839	EN
Hirola	*Beatragus hunteri*	Present	33	12	11,352	16,512	**3,405.7**	0.270	LC
		2080	0	0	0	0	**0.0**		CR/EX
Aders' duiker	*Cephalophus adersi*	Present	6	4	2,064	5,504	**88.3**	0.708	EN
		2080	0	0	0	0	**0.0**		CR/EX
Peter' duiker	*Cephalophus callipygus*	Present	2,179	579	749,576	796,704	**616,208.5**	0.044	LC
		2080	303	112	104232	154,112	**29,668.6**	0.282	LC
Jentink's duiker	*Cephalophus jentinki*	Present	311	93	106,984	127,968	**60,171.8**	0.129	LC
		2080	156	58	53,664	79,808	**14,991.9**	0.286	LC
White-bellied duiker	*Cephalophus leucogaster*	Present	3,608	964	1,241,152	1,326,464	**1,002,444.3**	0.048	LC
		2080	510	204	175,440	280,704	**38,749.3**	0.339	LC
Abbott's duiker	*Cephalophus spadix*	Present	19	10	6,536	13,760	**597.7**	0.537	VU
		2080	9	5	3,096	6,880	**238.0**	0.576	EN
Beira	*Dorcatragus megalotis*	Present	116	51	39,904	70,176	**6,505.0**	0.407	LC
		2080	83	36	28,552	49,536	**4,861.7**	0.397	LC
Speke's gazelle	*Gazella spekei*	Present	457	137	157,208	188,512	**87,714.8**	0.131	LC
		2080	377	109	129,688	149,984	**81,284.2**	0.105	LC
Nile Lechwe	*Kobus megaceros*	Present	324	97	111,456	133,472	**62,453.7**	0.130	LC
		2080	0	0	0	0	**0.0**		CR/EX
Silver dik-dik	*Madoqua piacentinii*	Present	102	42	35,088	57,792	**7,060.6**	0.360	LC
		2080	13	8	4,472	11,008	**247.5**	0.650	EN
Dama gazelle	*Nanger dama*	Present	836	251	287,584	345,376	**159,673.4**	0.132	LC
		2080	36	16	12,384	22,016	**1,949.47**	0.415	VU
Mountain nyala	*Tragelaphus buxtoni*	Present	21	11	7,224	15,136	**670.8**	0.534	VU
		2080	14	8	4,816	11,008	**338.1**	0.596	EN

*Table 6-4: Estimation of Area Of Occupancy (AOO) at 4km² (**bold**) based on scaling down from ≈344km² to 4km² using IUCN Standards and Petitions Subcommittee (2014) methodology. Species presented include species with no future range, no future protected range, and those with a future 4km² estimated AOO below 500km² (red) and 2,000km² (orange) indicating the threshold for IUCN 'Endangered' or "Critically Endangered" (EN,CR) and 'Vulnerable' (VU) statuses respectively under criteria B2 (IUCN Standards and Petitions Working Group, 2008). Results are based on the pessimistic ensemble approach results from chapters four and five. All other species are excluded as they have an estimated future AOO of >2000km². IUCN threat category codes: Least Concern (LC), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct (EX).*

Species		Generation length (years) - from linear model	Threshold % of range remaining in 80 years to trigger threatened status based on a rolling 30/50/80% (VU/EN/CR) loss of range every 3 generations			Projected range remaining under pessimistic approach	Projected IUCN threat category using criteria A3
			VU	EN	CR		
Addax	*Addax nasomaculatus*	7	24.01%	6.25%	0.16%	0.00%	CR
Dibatag	*Ammodorcas clarkei*	6	19.21%	4.17%	0.08%	2.07%	EN
Hirola	*Beatragus hunteri*	7	24.01%	6.25%	0.16%	0.00%	CR
Aders' duiker	*Cephalophus adersi*	5	15.13%	2.60%	0.02%	0.00%	CR
Peters' duiker	*Cephalophus callipygus*	5	15.13%	2.60%	0.02%	14.50%	VU
Jentink's duiker	*Cephalophus jentinki*	6	19.21%	4.17%	0.08%	40.93%	LC
White-bellied duiker	*Cephalophus leucogaster*	5	15.13%	2.60%	0.02%	13.50%	VU
Abbott's duiker	*Cephalophus spadix*	6	19.21%	4.17%	0.08%	63.64%	LC
Beira	*Dorcatragus megalotis*	6	19.21%	4.17%	0.08%	71.70%	LC
Speke's gazelle	*Gazella spekei*	5	15.13%	2.60%	0.02%	84.53%	LC
Nile Lechwe	*Kobus megaceros*	7	24.01%	6.25%	0.16%	0.00%	CR
Silver dik-dik	*Madoqua piacentinii*	5	15.13%	2.60%	0.02%	13.68%	VU
Dama gazelle	*Nanger dama*	6	19.21%	4.17%	0.08%	4.16%	EN
Mountain nyala	*Tragelaphus buxtoni*	8	30.87%	10.42%	0.59%	69.23%	LC

Table 6-5: Projected threat status based on an unconnected IUCN's A3 criteria (see methods). Generation lengths are the result of predictions from a linear model based on antelope generation times from the IUCN and predicted by adult mass. The thresholds are a cumulative reduction of range by 30, 50, and 80% every 3 generations over an 80 year period. Species displayed are those that have an assigned threat status based on the IUCN A3 criteria, those that have no future range or that have no protected area coverage in the future (see Table 6-6), and those that are classified under threat via criteria B2 (see Table 6-4). IUCN threat category codes: Least Concern (LC), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct (EX).

Africa ***Pessimistic approach*** ***A1B climate scenario***		Range within the African PAN	Species Range	
Species		**IUCN PAs in 2080 (cells)**	**Range in 2080(cells)**	**Percentage change (present to 2080)**
Addax	*Addax nasomaculatus*	0	0	-100
Hirola	*Beatragus hunteri*	0	0	-100
Aders' duiker	*Cephalophus adersi*	0	0	-100
Nile Lechwe	*Kobus megaceros*	0	0	-100
Dibatag	*Ammodorcas clarkei*	0	5	-97.94
Silver dik-dik	*Madoqua piacentinii*	0	13	-87.32
Beira	*Dorcatragus megalotis*	0	78	-28.30
Jentink's duiker	*Cephalophus jentinki*	0	145	-59.06
Speke's gazelle	*Gazella spekei*	0	377	-15.47
Abbott's duiker	*Cephalophus spadix*	5	8	-36.36
Mountain nyala	*Tragelaphus buxtoni*	9	9	-30.77
Peters' duiker	*Cephalophus callipygus*	13	293	-85.50
Dama gazelle	*Nanger dama*	17	36	-95.84
White-bellied duiker	*Cephalophus leucogaster*	41	483	-86.50

Table 6-6: The number of protected area cells, global range, and contraction of range for the 14 antelope species considered in this chapter ordered by number of cells protected by IUCN protected areas (PAs) and global range in 2080.

Table 6-7 details the number of species that may be encountered that are not currently within the focal species' predicted ranges (novel species). This is subdivided into connected cells and unconnected cells with significantly more novel species encountered in unconnected cells ($F_{1, 24}$=10.81; P=0.003). Table 6-8 details the number of cells that provide suitable climatic conditions for each of the 14 species at risk due to climate change or lack of protection. No species qualify for downgrading over time due to climate change based on IUCN category B2 (i.e. no species has a current AOO that would classify it as threatened, and a predicted expansion of range by 2080 that reduces that threat status). Below I consider each species individually, ordered by scientific name. Cells are described as core, connected, or unconnected cells based on whether they are found suitable under the pessimistic approach, the envelope approach, or the unconnected ensemble model respectively.

Focal species		Maximum number of novel species encountered	
		Connected cells	Unconnected cells
Addax	*Addax nasomaculatus*	1	1
Dibatag	*Ammodorcas clarkei*	5	6
Hirola	*Beatragus hunteri*	NA	4
Aders' duiker	*Cephalophus adersi*	NA	13
Peters' duiker	*Cephalophus callipygus*	3	7
Jentink's duiker	*Cephalophus jentinki*	1	8
White-bellied duiker	*Cephalophus leucogaster*	3	5
Abbott's duiker	*Cephalophus spadix*	3	7
Beira	*Dorcatragus megalotis*	4	9
Speke's gazelle	*Gazella spekei*	4	7
Nile Lechwe	*Kobus megaceros*	9	11
Silver dik-dik	*Madoqua piacentinii*	4	4
Dama gazelle	*Nanger dama*	2	6
Mountain Nyala	*Tragelaphus buxtoni*	1	7

Table 6-7: Maximum number of novel species the focal species might be expected to encounter in connected and unconnected cells. 'NA' represents species where no connected cells are available.

Table 6-9 presents the mean niche overlap details for each species according to range type (current, connected, and unconnected). This table shows the mean, minimum, and maximum values for each cell type (e.g. the mean represents the mean niche overlap values for all cells in the current, connected, or unconnected range). Kruskal-Wallis test compares the means of cells across all range types. Pairwise comparisons using Nemenyi post-hoc tests identify significant differences between range types. This highlights where range types may offer increased or reduced foraging competition. There was no significant difference in mean niche overlap between connected or unconnected cells ($F_{1, 24}$=0.122; P=0.73). Species specific details are found below. All references to threatened status (VU, EN, or CR), relate to the species' current IUCN status unless otherwise stated.

Species		Cell Type	Number of current cells where the target species is still present in 2080		Number of cells where the target species is the **only** species present in a cell (number of 10' grid cells) in 2080		Number of cells with an average mean niche overlap **lower than or equal** to the mean niche overlap found in the target species' 2080 range		Number of cells with an average mean niche overlap **greater than** the mean niche overlap found in the target species' 2080 range		
			Protected by IUCN PAs	Unprotected	Protected by IUCN PAs	Unprotected	Protected by IUCN PAs	Unprotected	Protected by IUCN PAs	Unprotected	Total 10' grid cells
Addax	*Addax nasomaculatus*	Existing	0	0							**0**
		Connected			0	0	15	117	39	230	**401**
		Unconnected			0	5	1	53	1	162	**222**
Dibatag	*Ammodorcas clarkei*	Existing	0	5							**5**
		Connected			0	0	0	0	0	407	**407**
		Unconnected			0	14	0	0	1	47	**62**
Hirola	*Beatragus hunteri*	Existing	0	0							**0**
		Connected			0	0	0	0	0	0	**0**
		Unconnected			0	1	5	24	0	0	**30**
Aders' duiker	*Cephalophus adersi*	Existing	0	0							**0**
		Connected			0	0	0	0	0	0	**0**
		Unconnected			0	1	0	0	194	2187	**2382**
Peters' duiker	*Cephalophus callipygus*	Existing	13	280							**293**
		Connected			0	0	19	126	16	106	**267**
		Unconnected			0	0	14	94	1	1	**110**
Jentink's duiker	*Cephalophus jentinki*	Existing	0	145							**145**
		Connected			0	0	1	31	0	36	**68**
		Unconnected			0	5	364	4818	9	205	**5401**
White-bellied duiker	*Cephalophus leucogaster*	Existing	41	442							**483**
		Connected			0	0	15	204	8	194	**421**
		Unconnected			0	0	9	96	2	14	**121**

TABLE CONTINUATION

Species		Cell Type	Number of current cells where the target species is still present in 2080		Number of cells where the target species is the **only** species present in a cell (number of 10' grid cells) in 2080		Number of cells with an average mean niche overlap **lower than or equal** to the mean niche overlap found in the target species' 2080 range		Number of cells with an average mean niche overlap **greater than** the mean niche overlap found in the target species' 2080 range		Total 10' grid cells
			Protected by IUCN PAs	Unprotected	Protected by IUCN PAs	Unprotected	Protected by IUCN PAs	Unprotected	Protected by IUCN PAs	Unprotected	
Abbott's duiker	*Cephalophus spadix*	Existing	5	3							**8**
		Connected			0	0	1	3	0	10	**14**
		Unconnected			0	0	22	51	57	165	**295**
Beira	*Dorcatragus megalotis*	Existing	0	78							**78**
		Connected			0	0	0	442	0	516	**958**
		Unconnected			9	408	17	1599	5	449	**2487**
Speke's gazelle	*Gazella spekei*	Existing	0	377							**377**
		Connected			0	0	0	203	0	136	**339**
		Unconnected			7	223	0	24	12	1036	**1302**
Nile Lechwe	*Kobus megaceros*	Existing	0	0							**0**
		Connected			0	0	2	12	0	1	**15**
		Unconnected			0	0	51	265	0	4	**320**
Silver dik-dik	*Madoqua piacentinii*	Existing	0	13							**13**
		Connected			0	0	0	2	0	52	**54**
		Unconnected			0	0	0	15	1	3	**19**
Dama gazelle	*Nanger dama*	Existing	17	19							**36**
		Connected			0	4	33	1241	54	405	**1737**
		Unconnected			0	34	1	172	0	423	**630**
Mountain Nyala	*Tragelaphus buxtoni*	Existing	9	0							**9**
		Connected			0	0	5	1	3	1	**10**
		Unconnected			0	0	6	27	5	36	**74**

Table 6-8: The number of Existing, Connected, and Unconnected cells suitable for species in 2080. These are split by IUCN protection status and by mean niche overlap comparison with the species' current mean niche overlap (Connected and Unconnected only).

Species		Range type	Mean niche overlap for each species' range based on range type (current, connected, unconnected)				Kruskal-Wallis rank sum test across all range types				
			Mean	Standard deviation	Minimum	Maximum	χ^2	P	Significance between ranges (Nemenyi post-hoc Kruskal-Wallis test)		
									Current-Connected	Current-Unconnected	Connected-Unconnected
Addax	*Addax nasomaculatus*	Current range	0.585	0.000	0.585	0.585	165.903	<0.001	<0.001	<0.001	0.61
		Connected future	0.674	0.063	0.585	0.756					
		Unconnected future	0.681	0.057	0.460	0.756					
Dibatag	*Ammodorcas clarkei*	Current range	0.889	0.017	0.820	0.950	379.612	<0.001	<0.001	<0.001	<0.001
		Connected future	0.927	0.016	0.890	0.954					
		Unconnected future	0.942	0.013	0.923	0.961					
Hirola	*Beatragus hunteri*	Current range	0.570	0.029	0.453	0.587	41.380	<0.001	NA	<0.001	NA
		Connected future									
		Unconnected future	0.436	0.109	0.286	0.553					
Aders' duiker	*Cephalophus adersi*	Current range	0.244	0.071	0.161	0.285	8.504	0.004	NA	0.004	NA
		Connected future									
		Unconnected future	0.673	0.109	0.123	0.896					
Peters' duiker	*Cephalophus callipygus*	Current range	0.682	0.054	0.409	0.858	261.933	<0.001	0.085	<0.001	<0.001
		Connected future	0.668	0.068	0.447	0.768					
		Unconnected future	0.469	0.127	0.142	0.734					
Jentink's duiker	*Cephalophus jentinki*	Current range	0.783	0.035	0.701	0.927	627.686	<0.001	0.002	<0.001	<0.001
		Connected future	0.762	0.049	0.672	0.863					
		Unconnected future	0.690	0.085	0.084	0.914					
White-bellied duiker	*Cephalophus leucogaster*	Current	0.715	0.045	0.515	0.869	243.581	<0.001	<0.001	<0.001	<0.001
		Connected future	0.693	0.052	0.558	0.793					
		Unconnected future	0.532	0.148	0.209	0.739					
Abbott's duiker	*Cephalophus spadix*	Current range	0.397	0.099	0.040	0.529	7.454	0.024	0.039	0.034	0.58
		Connected future	0.504	0.113	0.375	0.700					
		Unconnected future	0.467	0.122	0.040	0.756					

Beira	*Dorcatragus megalotis*	Current range	0.892	0.032	0.753	0.982	474.346	<0.001	0.99	<0.001	<0.001
		Connected future	0.895	0.027	0.773	0.943					
		Unconnected future	0.843	0.081	0.313	0.962					
Speke's gazelle	*Gazella spekei*	Current range	0.824	0.013	0.803	0.883	1281.246	<0.001	0.68	<0.001	<0.001
		Connected future	0.822	0.012	0.774	0.848					
		Unconnected future	0.873	0.022	0.768	0.947					
Nile Lechwe	*Kobus megaceros*	Current range	0.923	0.092	0.716	0.999	419.440	<0.001	<0.001	<0.001	0.470
		Connected future	0.667	0.117	0.491	0.931					
		Unconnected future	0.590	0.144	0.185	1.000					
Silver dik-dik	*Madoqua piacentinii*	Current range	0.819	0.071	0.714	0.903	77.455	<0.001	<0.001	1	<0.001
		Connected future	0.924	0.036	0.749	0.942					
		Unconnected future	0.800	0.088	0.693	0.961					
Dama gazelle	*Nanger dama*	Current range	0.896	0.013	0.868	0.946	695.919	<0.001	<0.001	<0.001	<0.001
		Connected future	0.902	0.025	0.842	0.978					
		Unconnected future	0.930	0.026	0.827	0.946					
Mountain Nyala	*Tragelaphus buxtoni*	Current range	0.599	0.118	0.342	0.854	1.562	0.458	0.87	0.74	0.51
		Connected future	0.579	0.024	0.557	0.604					
		Unconnected future	0.625	0.129	0.311	0.988					

Table 6-9: Species mean niche overlap details (mean, s.d., min., max.) based on current (IUCN distribution), connected future range (envelope approach), and unconnected future range (unconnected from current distribution). The values relate to the mean/standard deviation/minimum/maximum of all mean niche overlap values (Pianka's niche overlap index) for all cells within that range type. Values exclude cells where the target species is the only antelope species present (mean niche overlap equals 0). Kruskal-Wallis rank sum test indicates the significance in difference between cell types. Nemenyi post-hoc test identifies the significant relationships between range types.

Addax (Figure 6-2)

Predicted to have no core range under the pessimistic approach, the addax (CR) has connected areas suitable to the west of Africa, and unconnected areas to the east. These additional areas include 56 cells where IUCN protection is available, 54 of these are in connected areas. The mean niche overlap in connected and unconnected cells is significantly higher than the current range ($P<0.001$ for both connected and unconnected cells). No difference was found between the connected and unconnected ($P=0.61$). Fifteen (of 54) protected cells are in areas with lower than average mean niche overlap.

The PAs offering protection to the addax in the connected areas (Ahaggar national park in Algeria, and Aïr de Ténéré in Niger) are largely divided between two areas to the north west of Lake Chad (Niger and Algeria; Figure 6-2). Five unconnected cells will be free of all antelopes but suitable for the addax, albeit they are currently unprotected. In total 623 cells provide suitable habitat.

Dibatag (Figure 6-3)

The dibatag (VU) has a highly restricted core range with only five unprotected cells suitable. Under the envelope approach this is expanded by 407 connected cells available, all of which are unprotected and have greater niche overlap than present; these are largely restricted to Somalia. There are 62 unconnected cells available; only one of these offers protection (Dombe Grande reserve) while 14, situated on the opposite side of the continent, would allow the species to have no antelope competition. All cells, except those where the dibatag would be without competition, provide higher niche overlap than present. In total 474 cells provide suitable habitat.

The mean niche overlap of connected and unconnected areas is significantly higher than the current range ($P<0.001$ for both connected and unconnected cells), and the unconnected range was higher than the connected range ($P<0.001$). The mean niche overlap in the current range is the second highest of the antelope considered here. In total 474 cells provide suitable habitat. The dibatag would potentially encounter five novel species in connected cells and six in unconnected cells.

Hirola (Figure 6-4)

The hirola (CR) is one of two species that will rely upon unconnected cells as it has no future range under either pessimistic or envelope approaches. It is limited to 30 unconnected cells

split into two areas; the first is to the northwest of its existing range, the second is on the west coast of Angola. Unconnected cells offer lower niche overlap than at present (χ^2=41.380; P<0.001), but only five are currently protected. Up to four novel species are found in those PAs to the northwest, whereas the area to the far west would introduce only one new species.

Aders' duiker (Figure 6-5)

Aders' duiker (CR) also has no suitable areas under the pessimistic or envelope approaches due to the habitat filter restricting dispersal through grassland surrounding its current range. This duiker's original distribution was limited to six cells, three of which were on the island of Zanzibar. In the future there are large areas of suitable climate across the tropical forest region of Africa. In total 2,382 unconnected cells are available with 194 offering IUCN protection, an area in the Selous Game reserve being the nearest to its current range. These unconnected areas present a higher mean niche overlap than present (χ^2=8.504; P=0.004) due to very low overlap in its present range (mean=0.244). Areas to the east of Africa, nearer its existing range, offer lower niche overlap with fewer novel species present. Aders' duiker could potentially encounter 13 novel species in central Africa. This is the highest of the 14 species considered here, the majority of those being other duiker species.

Peters' duiker (Figure 6-6)

Peters' duiker (*Cephalophus callipygus*) retains 293 cells in its current range with 13 cells offering IUCN protection. The connected and unconnected cells are located largely in the centre of Africa. The connected and unconnected areas are separated by incompatible habitat and areas without suitable climate. Suitable areas include 50 cells within the IUCN PAs. The current and connected ranges do not differ significantly in mean niche overlap (P=0.085). However, the mean niche overlap of unconnected cells is lower than within the current and connected cells (P<0.001 for both current and connected cells).

Jentink's duiker (Figure 6-7)

There are 145 cells remaining of the Jentink's duiker's range largely in Liberia and Sierra Leone, but none have IUCN protection. A wide expanse of central Africa provides suitable conditions totalling 5,614 cells. This includes 68 connected cells with one offering IUCN protection. The majority of the suitable range is therefore in unconnected areas with 373 cells providing protection. 364 of these are in areas with lower mean niche overlap than the present range, and there is significantly lower niche overlap in these new areas (connected: P=0.002; unconnected: p<0.001). There is also a lower mean niche overlap in unconnected

cells compared to connected cells (P<0.001). However, up to 8 novel species may be encountered in those unconnected areas. Five unconnected cells provide suitable conditions with no antelope competition on islands in the Bijagós archipelago. While none of these islands have IUCN protected areas, three of the cells provide the closed forest habitat required for Jentink's duiker. These cells form part of the Parque Nacional de Orango (IBAP, 2013), but it is unclear what level of protection is provided to the area.

White-bellied duiker (Figure 6-8)

The white-bellied duiker has a large contraction of range which divides into two, leaving an area to the west (Cameroon, Gabon, and Congo), and an area in central Africa (eastern areas of Democratic Republic of Congo (DRC)). There are 41 of 442 core cells remaining that have IUCN protection, largely in the eastern part of the range. Suitable conditions are found in 421 connected and 121 unconnected cells and these include a further 34 areas in PAs. The new areas offer lower mean niche overlap than the current range (P<0.001 for both connected and unconnected cells) and unconnected cells are lower than connected cells (P<0.001).

Abbott's duiker (Figure 6-9)

Abbott's duiker (EN) has nine core cells remaining with six offering protection. A further 14 connected cells, including one with protection, are available with four having lower mean niche overlap than present. Abbott's duiker has the second lowest mean niche overlap (0.397) in its current range which includes the submontane and high montane forests of Tanzania (Moyer *et al.*, 2008). New areas would have significantly higher niche overlap than current cells (P<0.001 for both connected and unconnected) with no difference between connected and unconnected (P=0.58). There are 295 unconnected cells ranging from South Africa to Ethiopia. Seventy-nine of these cells offer protection with the largest areas of protection found in Tanzania and Ethiopia (including Bale mountains).

Beira (Figure 6-10)

Beira (VU) are currently found in northern Somalia and possibly Ethiopia (Heckel *et al.*, 2008). The core range retains the majority of its current distribution (78 cells) while the connected cells extend this to the south with 958 cells, all of which are unprotected. The unconnected cells offer 2,487 new locations on Africa's north and west coastal areas outside of the tropical wetland areas at low latitudes. The unconnected cells include 31 IUCN protected cells and 417 cells where no other species are currently projected to be present. With such extensive areas of unconnected cells across the continent the beira would experience up to nine novel

species. The current range has a high mean niche overlap (0.892 ±0.032) which is similar to the connected cells (P=0.99). Both current and connected are significantly higher than the unconnected cells (P<0.001 for both current and connected).

Speke's gazelle (Figure 6-11)

Speke's gazelle's (EN) range demonstrates close similarities to the beira except that it has a narrower climatic niche breadth. This is demonstrated by the fact that the beira occupies largely the same area as the Speke's gazelle but the beira has a larger number of unconnected cells. Speke's gazelle is restricted to Somalia and contracts to 377 cells under the pessimistic approach. There is no protection for the species in Somalia, nor in the species' connected range of 339 cells which expands to include eastern areas of Ethiopia. 1,302 unconnected cells establish suitable areas along the west and north coasts of Africa similar to the beira. Much of the unconnected area has no novel species except for the area in the south west. However, Namibia presents areas that would be without any other antelopes, and which would also be suitable for the beira. The connected cells are located close to the existing cells as with the dibatag, beira, and to a lesser extent the silver dik-dik, suggesting relatively stable climatic conditions in this area. The current range cells mean niche overlap is similar to the connected cells (P=0.68). Both current and connected are significantly lower than the unconnected cells (P<0.001 for both current and connected cells).

Nile lechwe (Figure 6-12)

The pessimistic approach leaves no suitable areas for Nile lechwe. Two of 15 connected cells are covered by the IUCN protected area network. The unconnected area provides 320 cells with 50 offering protection. The Nile lechwe exhibits the highest mean niche overlap in its current range (mean 0.923) and new areas have significantly lower overlap (P<0.001 for both connected and unconnected). The new areas are largely in Eastern Africa and include parts of Ethiopia, Kenya, Tanzania, and Mozambique. These areas include long strips of suitable conditions along with smaller fragmented areas. The largest protected areas are found in Ethiopia. The Nile lechwe has the potential to overlap with up to nine novel species in the connected cells, and eleven in the unconnected areas.

Silver dik-dik (Figure 6-13)

The silver dik-dik currently has no threatened status due to lack of data. Under the pessimistic approach the species will be left with 13 unprotected cells. The 54 connected cells expand the species' range to the north further into Somalia which offers no protected

areas. 19 unconnected cells are available and are largely found in Angola; only one offers protection (Dombe Grande reserve). The current cells have similar mean niche overlap than the unconnected cells (P=1), while connected cells have significantly higher overlap than current cells (P<0.001).

Dama gazelle (Figure 6-14)

Dama gazelle (CR) persist in only 36 cells from its current range of which 17 fall within the IUCN protected area network, this represents a 95.9% contraction of range. The envelope approach predicts an expansion of range to a further 1,737 connected cells including four without other antelope species, and 87 with IUCN protection in Algeria. The connected cells have become fragmented into separate areas ranging from the east coast to the west coast, north of the equator. There are 630 unconnected cells present, but only one offers IUCN protection. The unconnected areas are towards the north of Africa in Algeria, Tunisia, and Libya. They also include a small area in Somalia and a small area on the southern border between Namibia and South Africa. New areas have higher mean niche overlap than the current distribution (P<0.001 for both connected and unconnected ranges). The unconnected cells have higher niche overlap than connected cells (P<0.001).

Mountain nyala (Figure 6-15)

The endangered mountain nyala is indigenous to Ethiopia and sees its current range contract to nine grid cells, all of which are protected by IUCN PAs. Mountain nyala are found in highlands, mainly around the Bale Mountains National Park (Evangelista *et al.*, 2008). These areas of high elevation offers relatively cool coldest and hottest temperatures. Ten connected and 74 unconnected cells offer suitable conditions. The connected cells are in Ethiopia, with the unconnected cells in highland areas of Kenya, Tanzania, DRC, and the Drakensberg mountains in Lesotho/South Africa. There is no significant difference in the mean niche overlap between any of the range types (all: P>0.5).

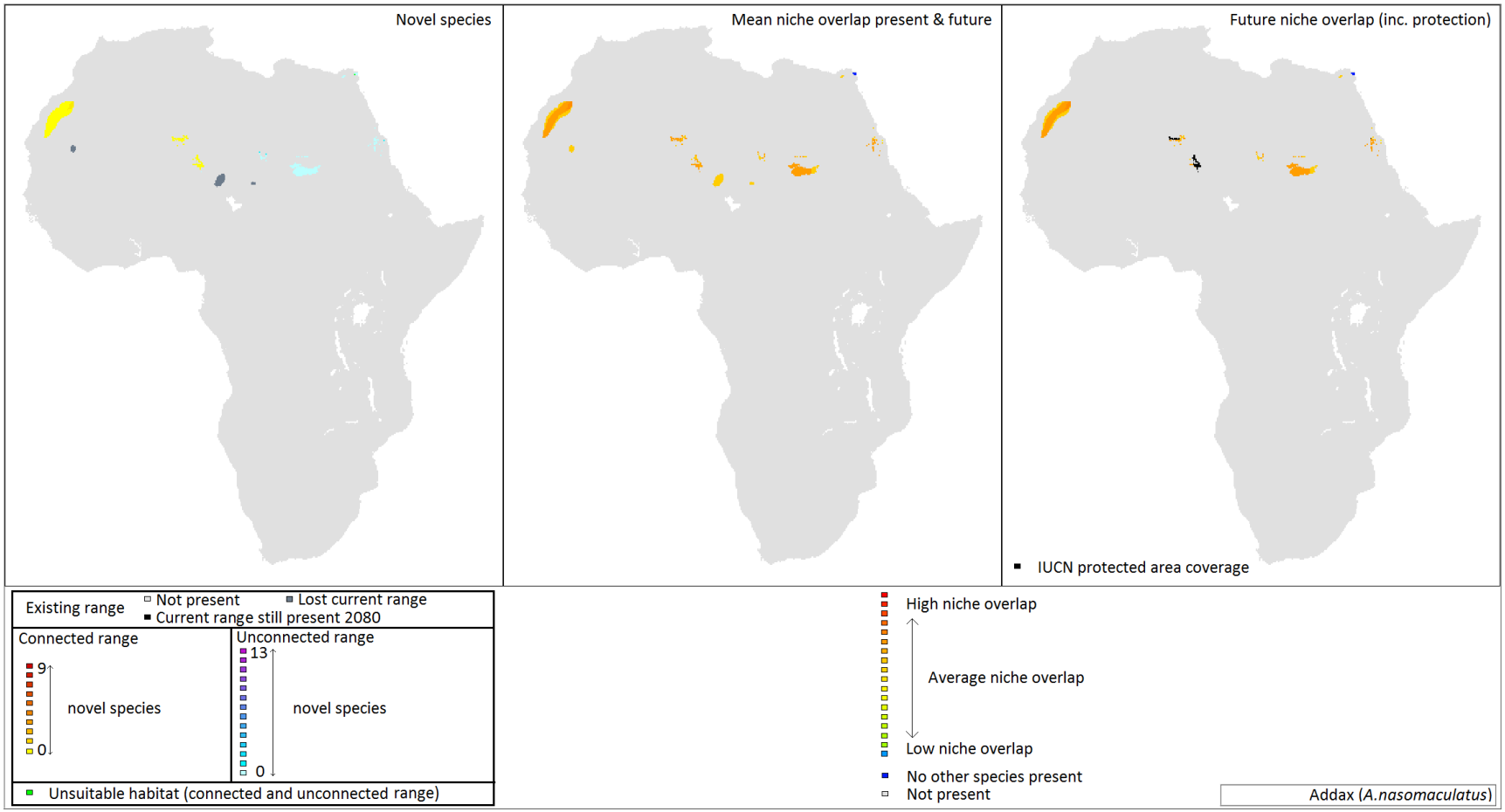

Figure 6-2: Ensemble projected range (A1B climate scenario) for addax. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

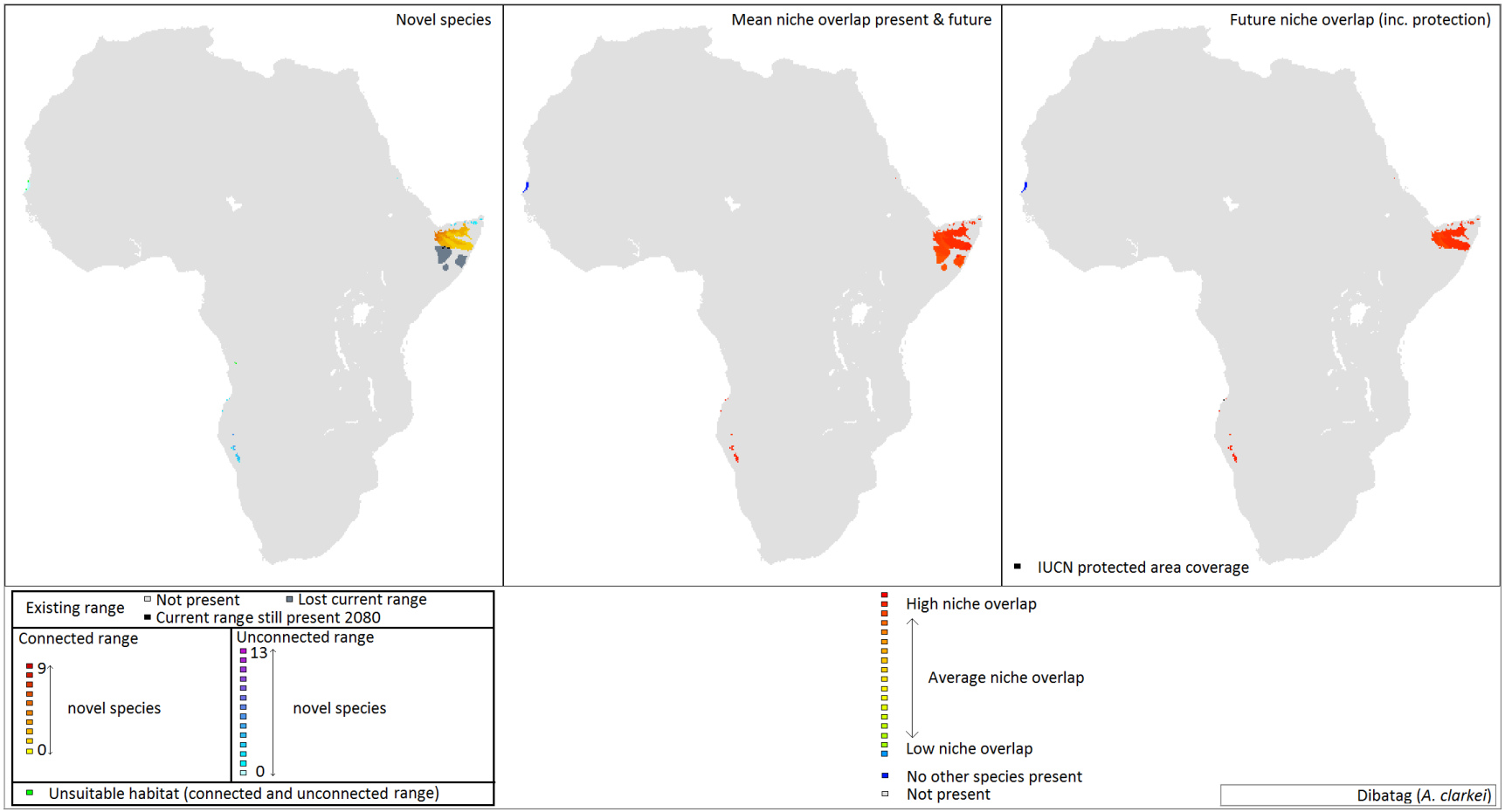

Figure 6-3: Ensemble projected range (A1B climate scenario) for dibatag. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

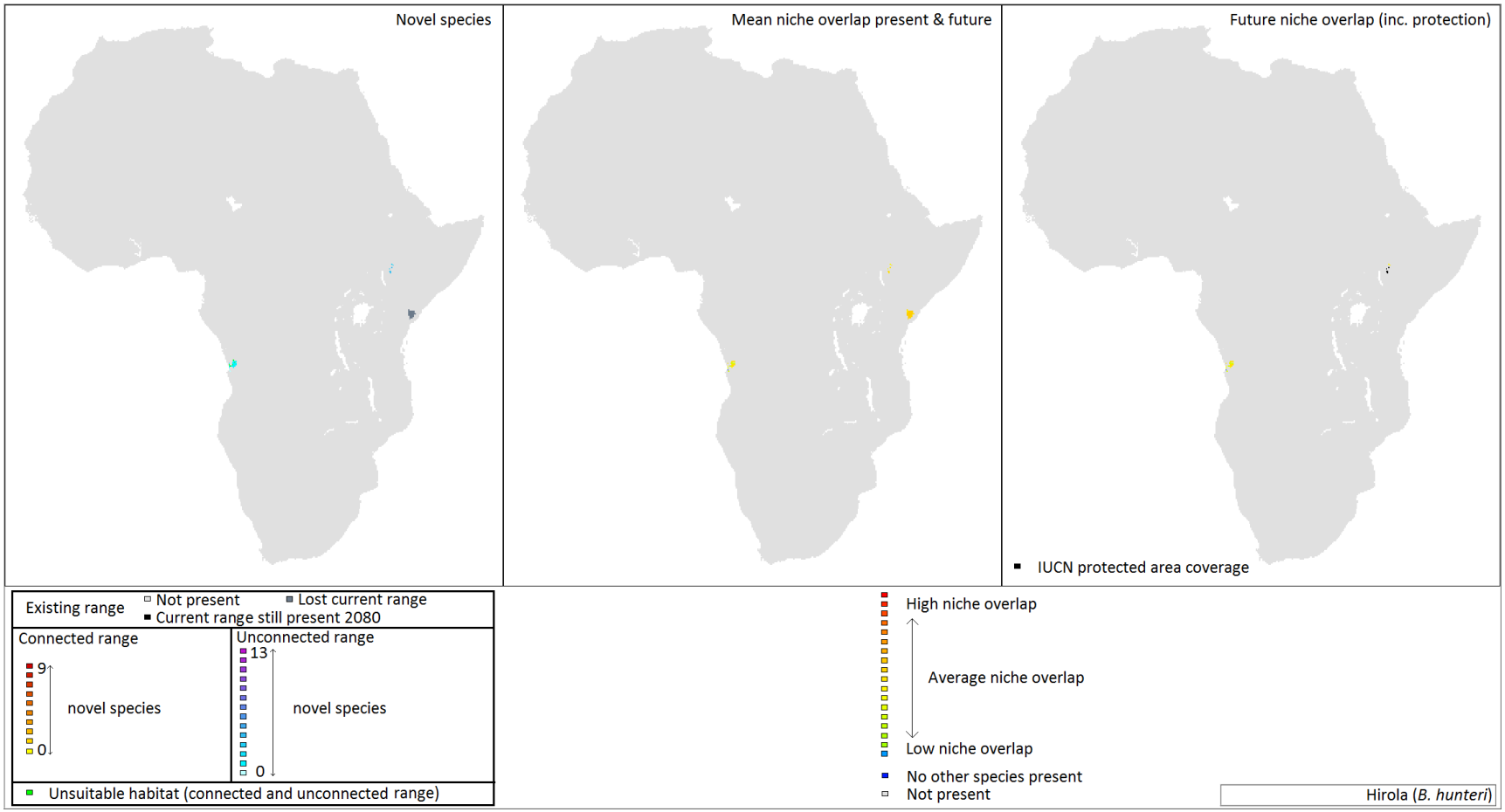

Figure 6-4: Ensemble projected range (A1B climate scenario) for hirola. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

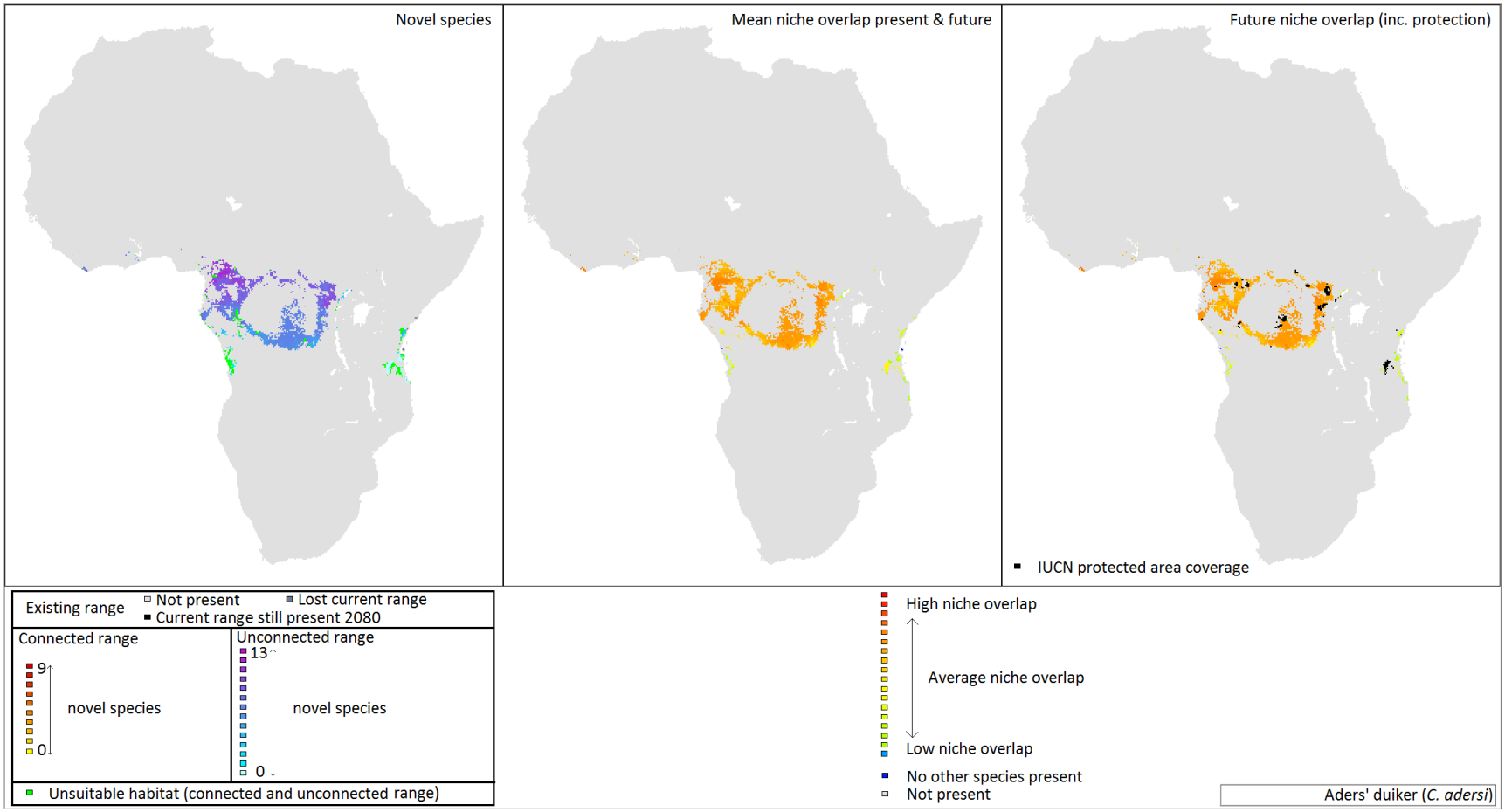

Figure 6-5: Ensemble projected range (A1B) for Aders' duiker. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

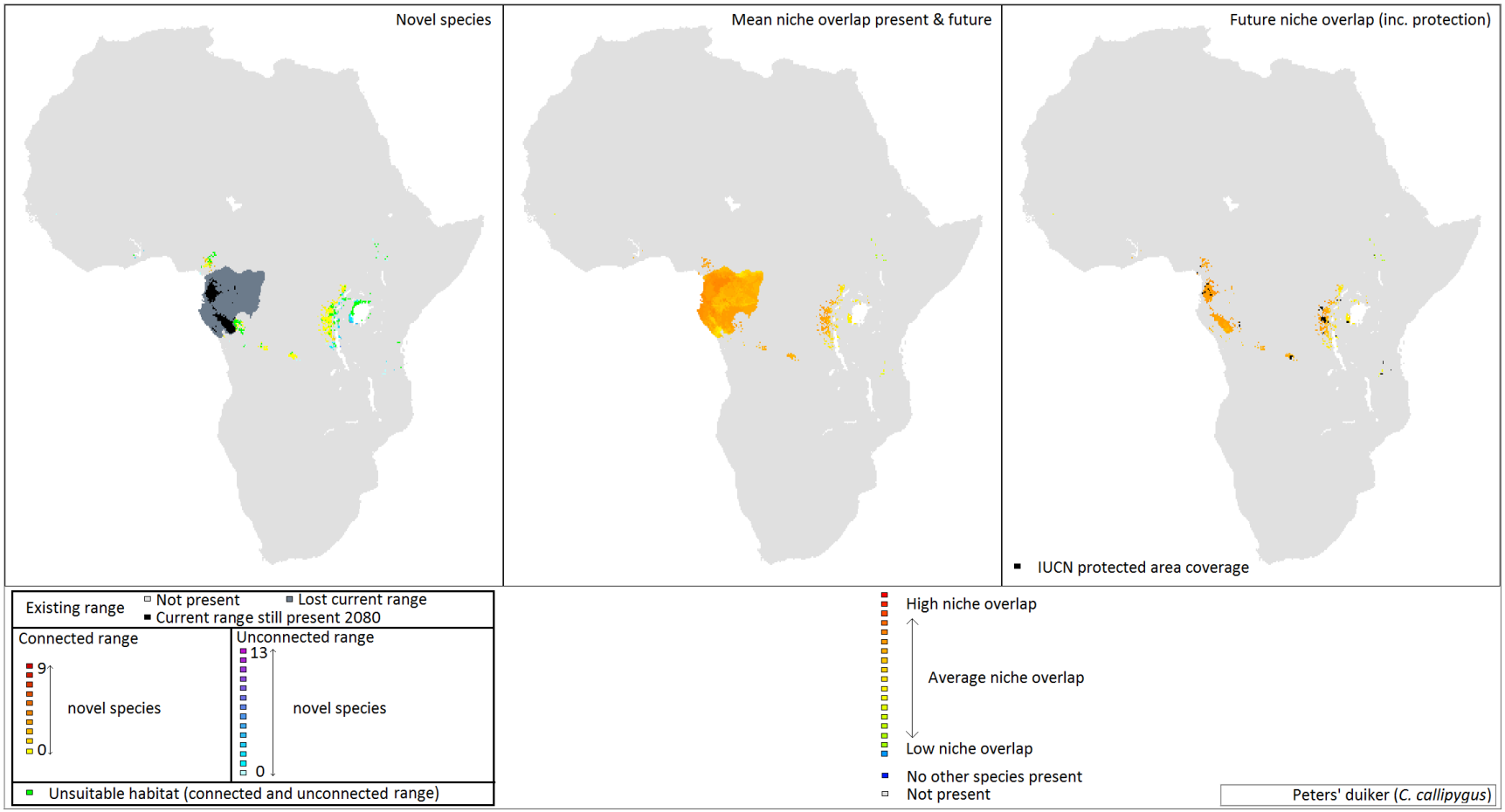

Figure 6-6: Ensemble projected range (A1B) for Peters' duiker. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

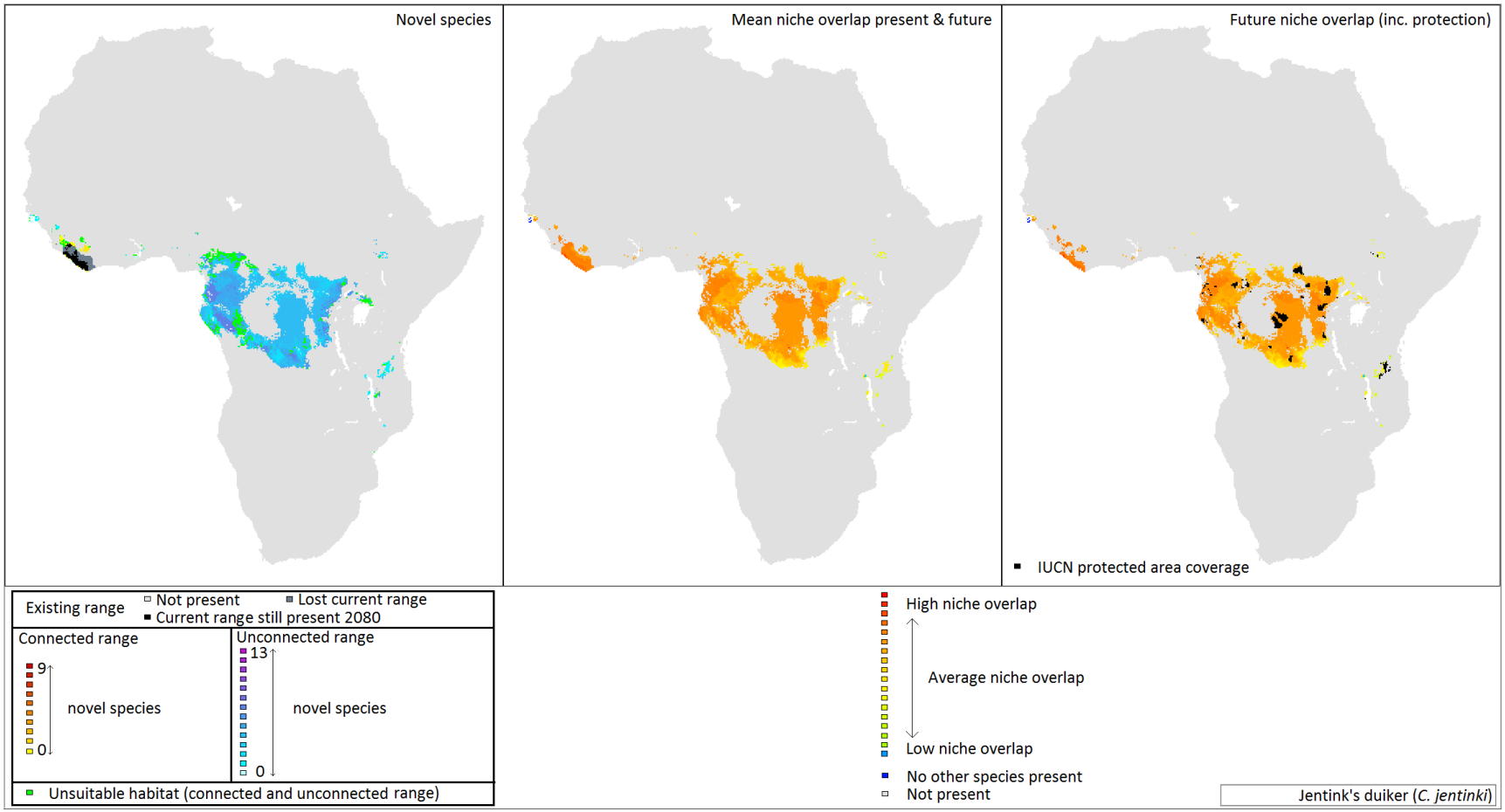

Figure 6-7: Ensemble projected range (A1B) for Jentink's duiker. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

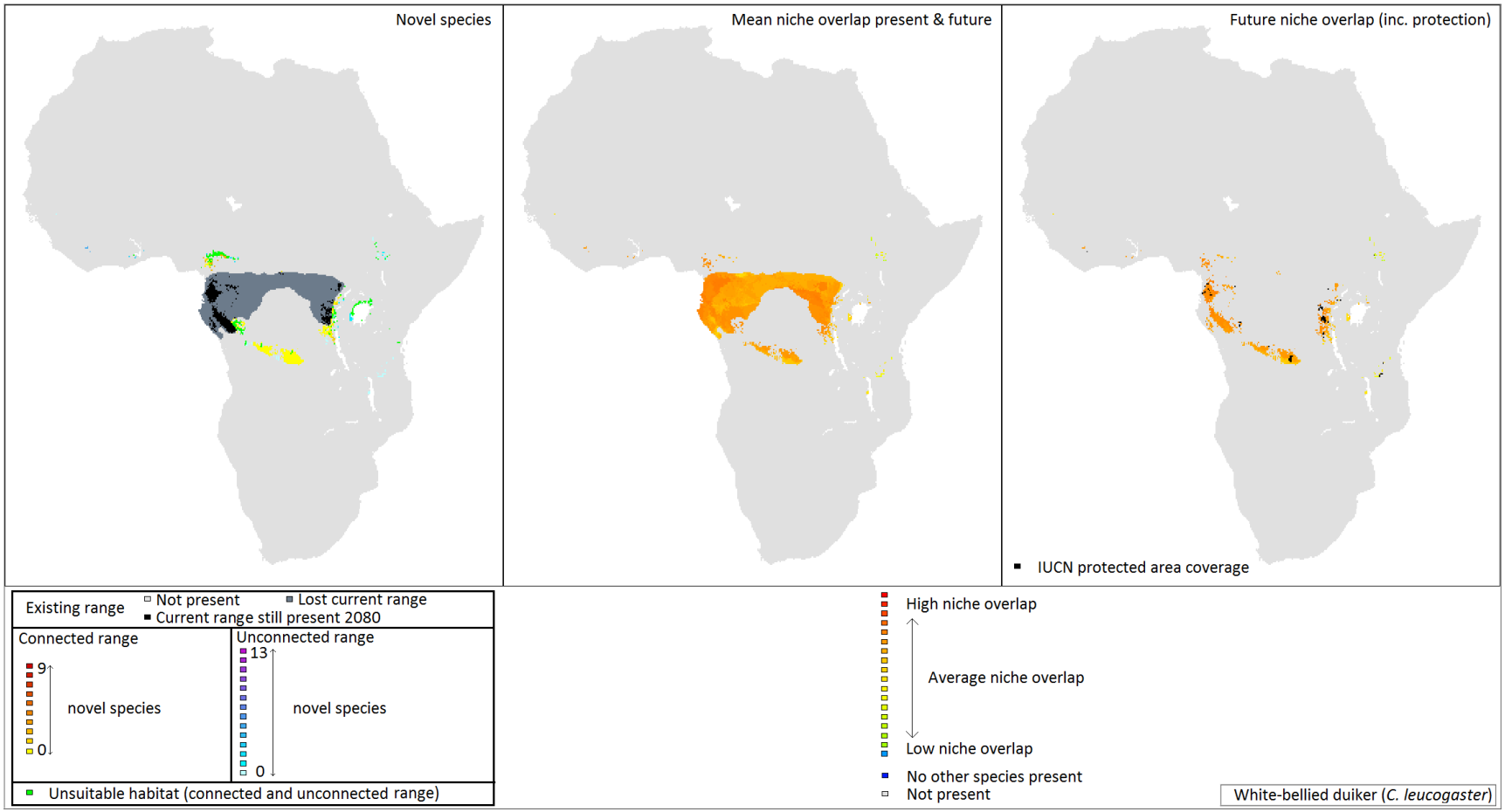

Figure 6-8: Ensemble projected range (A1B) for white-bellied duiker. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

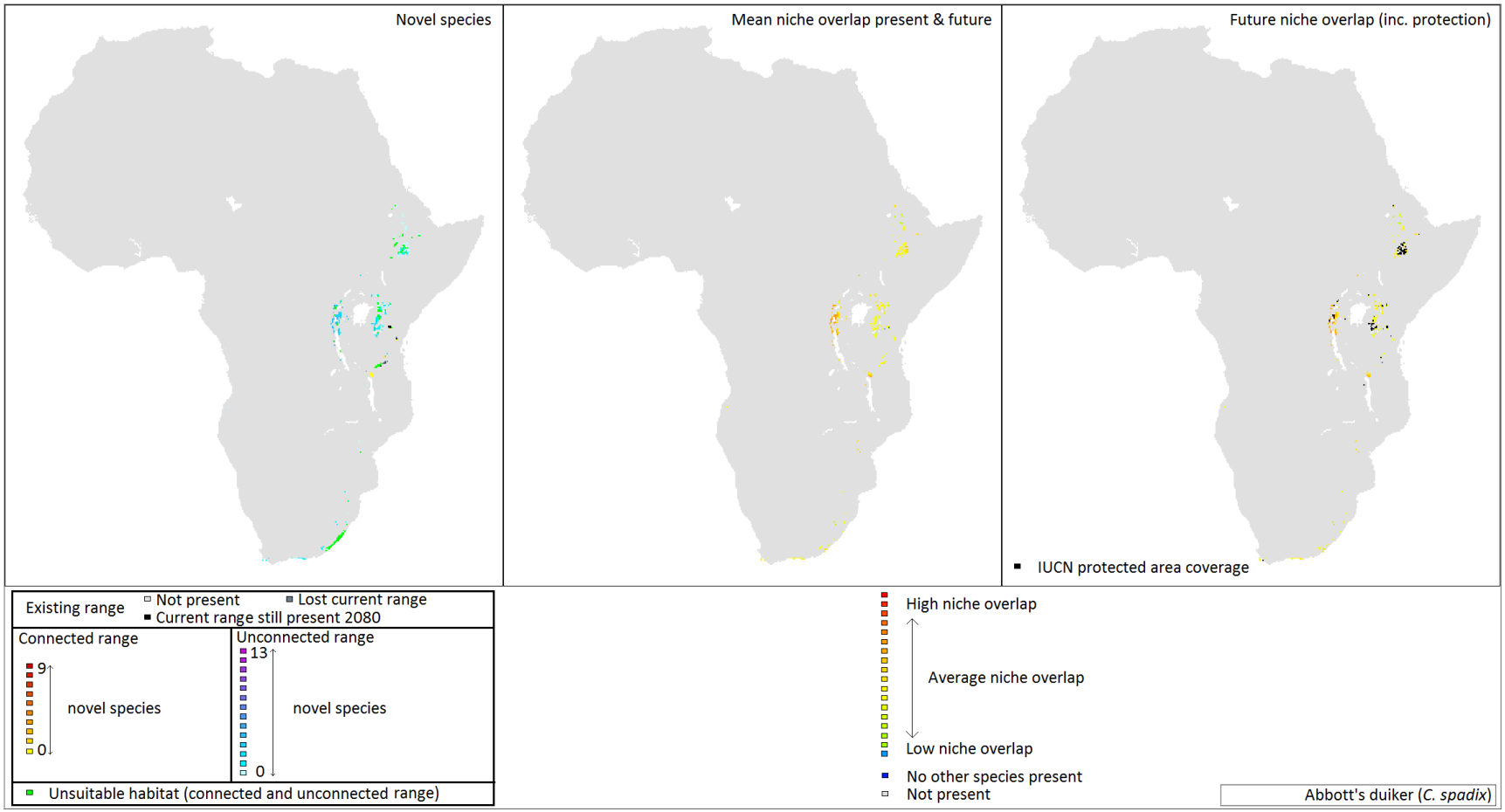

Figure 6-9: Ensemble projected range (A1B) for Abbott's duiker. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

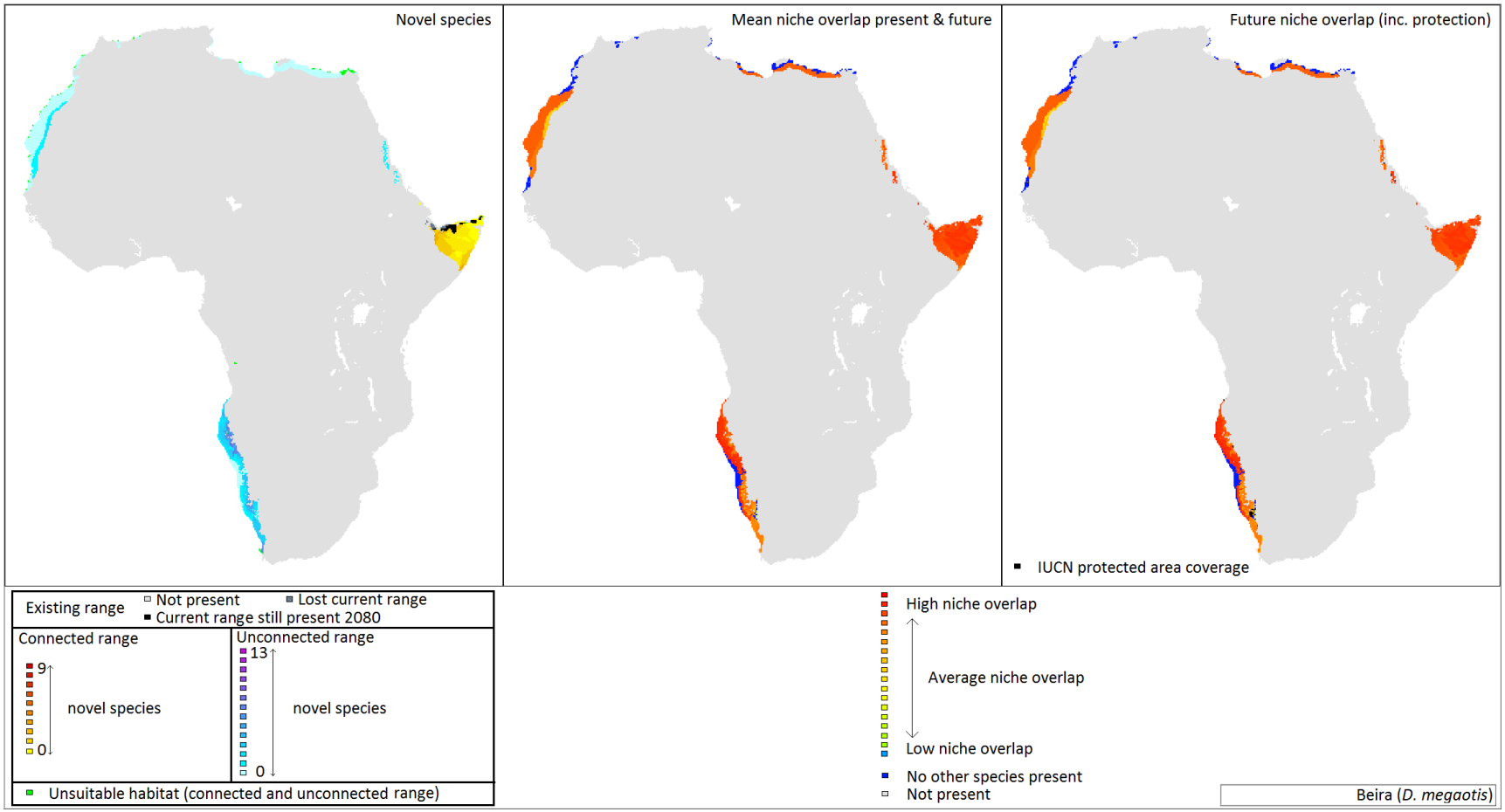

Figure 6-10: Ensemble projected range (A1B) for beira. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

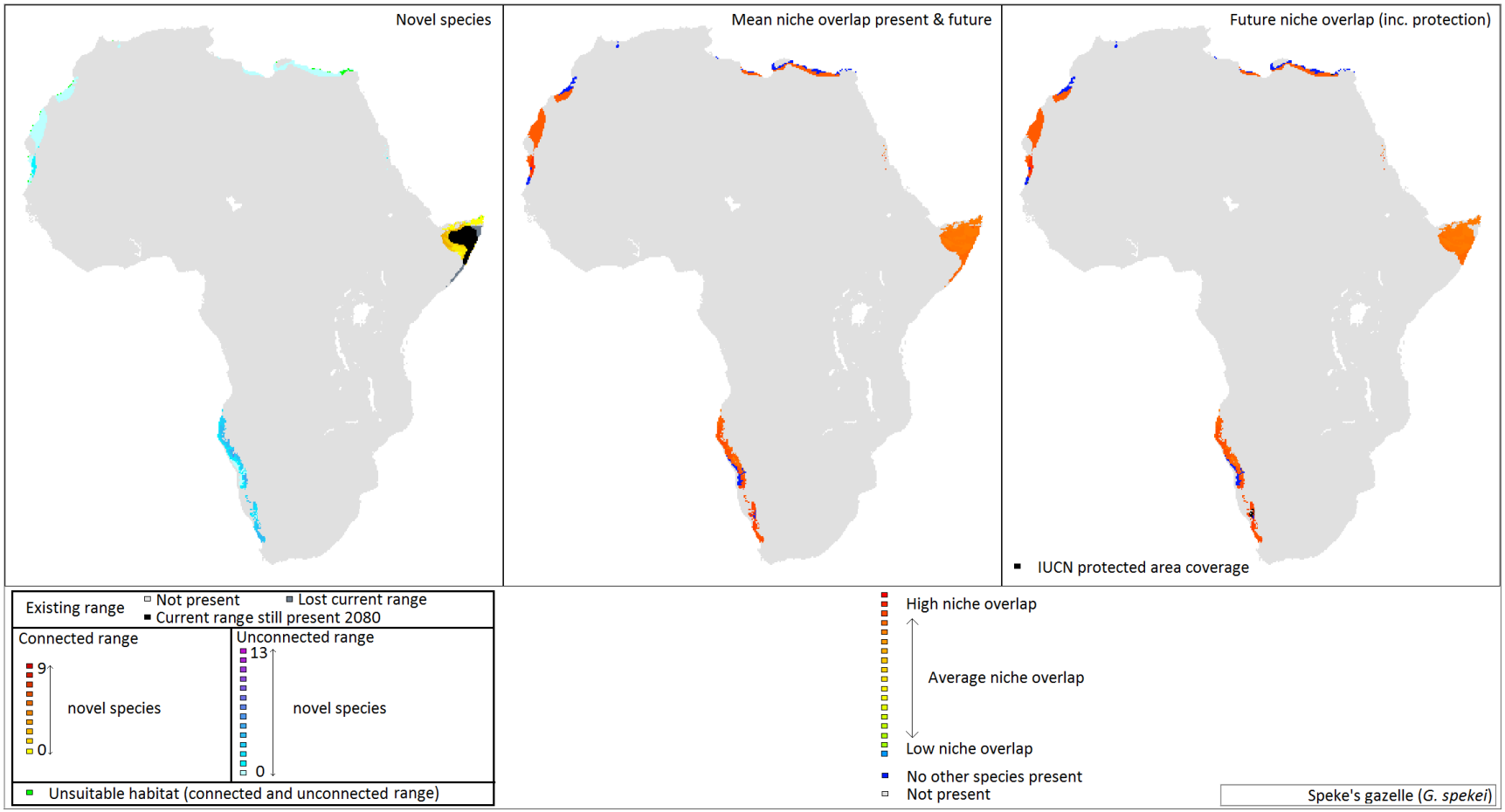

Figure 6-11: Ensemble projected range (A1B) for Speke's gazelle. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

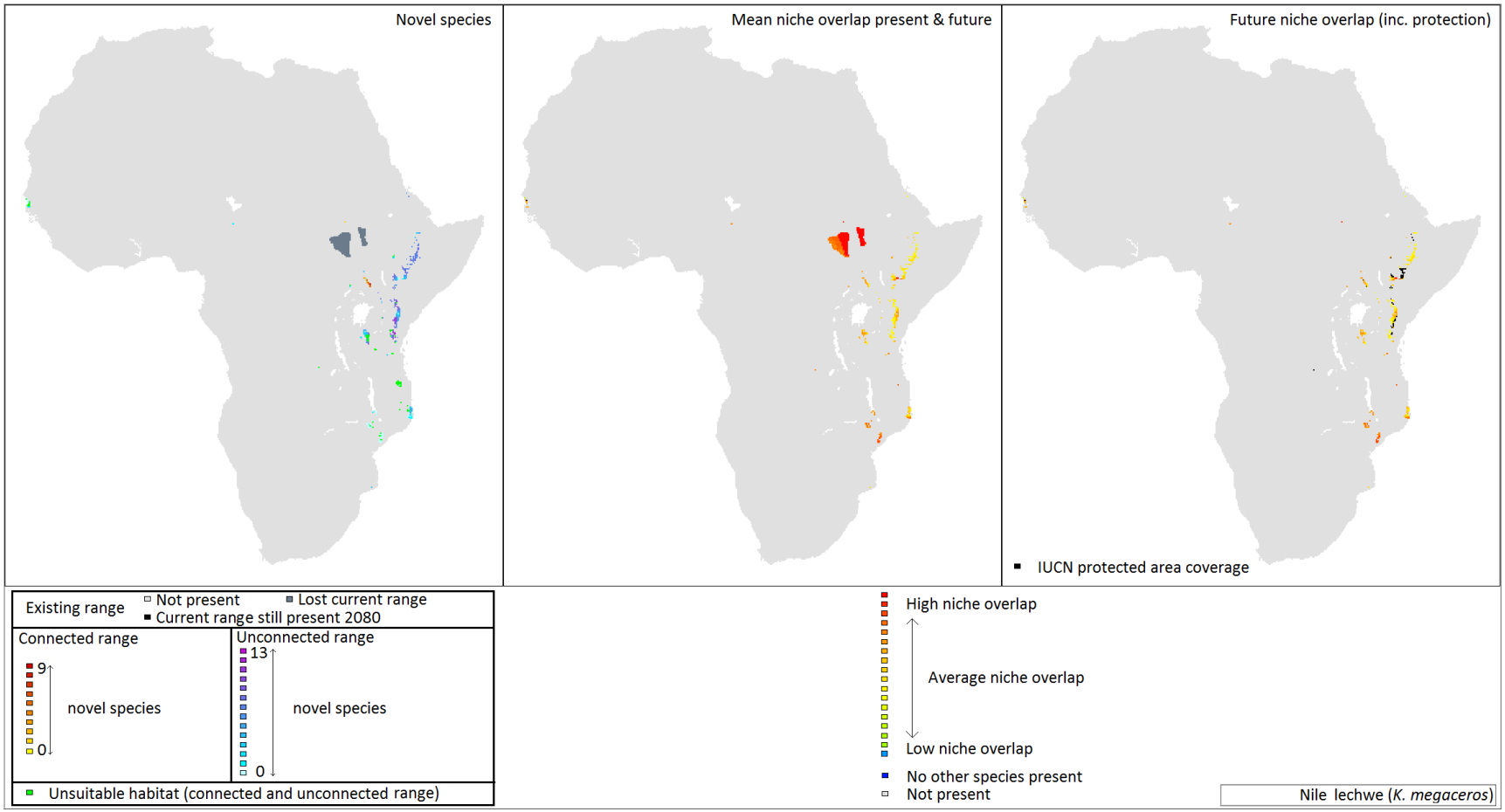

Figure 6-12: Ensemble projected range (A1B) for Nile lechwe. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

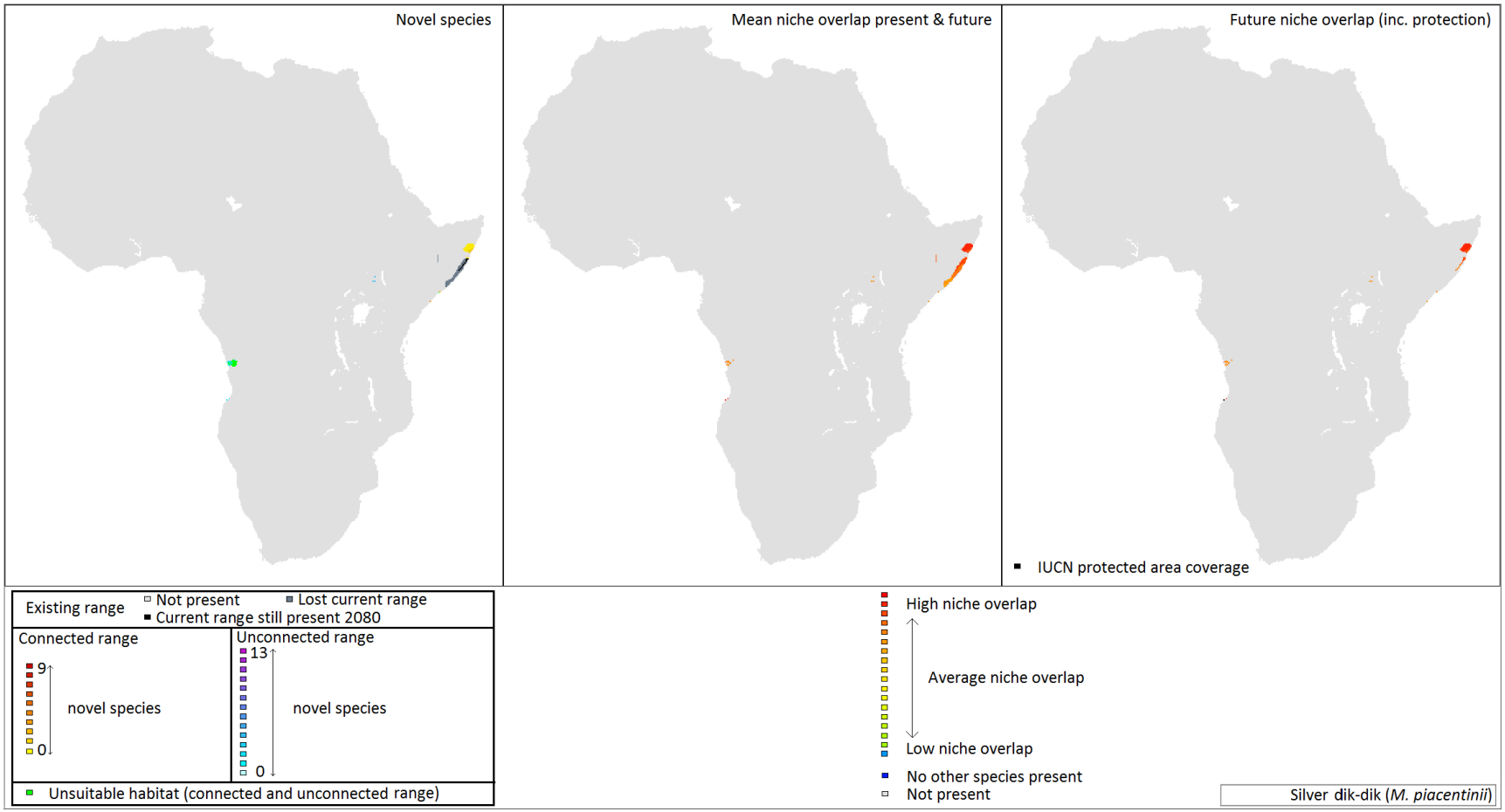

Figure 6-13: Ensemble projected range (A1B) for silver dik-dik. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

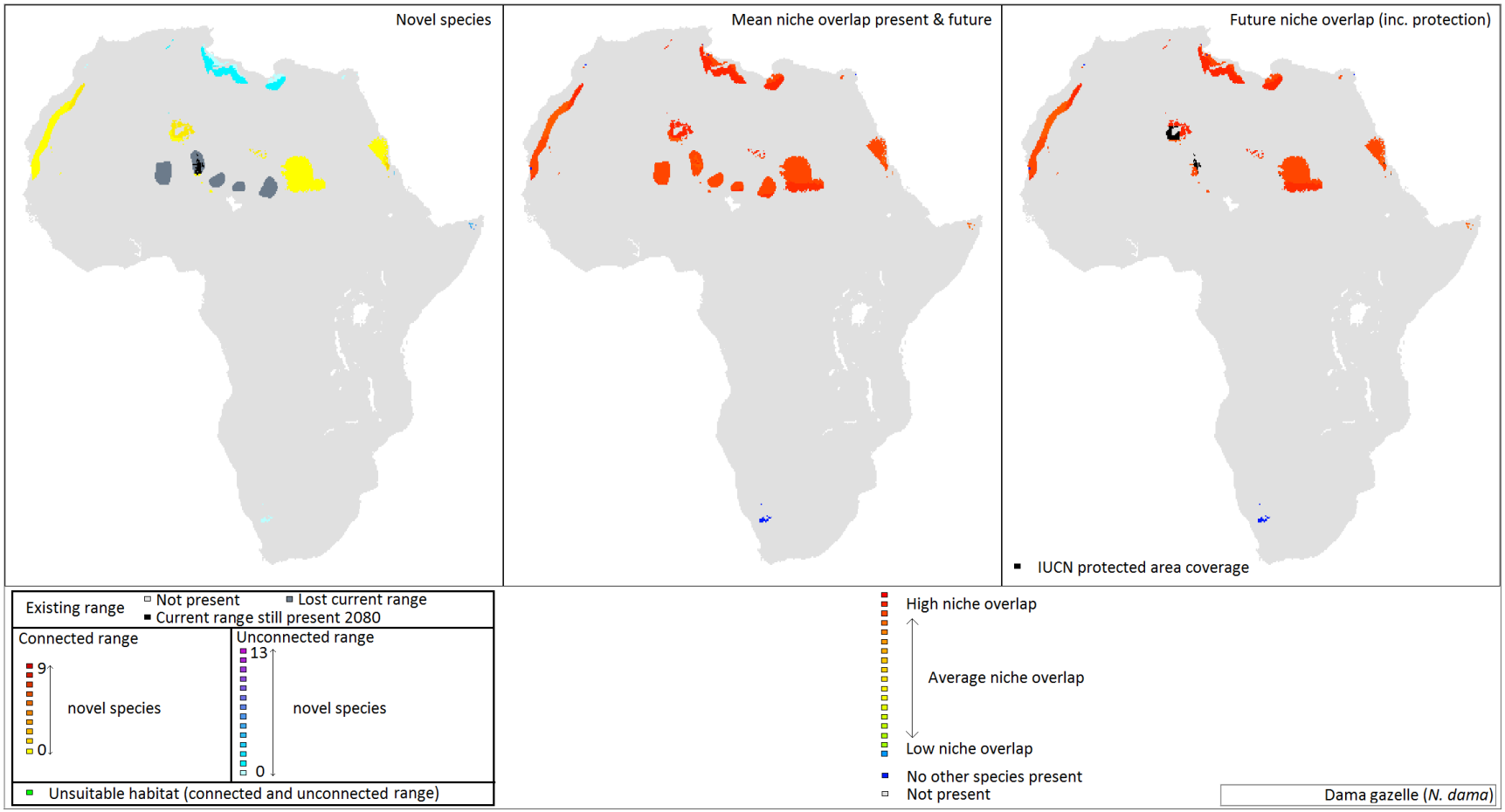

Figure 6-14: Ensemble projected range (A1B) for the dama gazelle. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

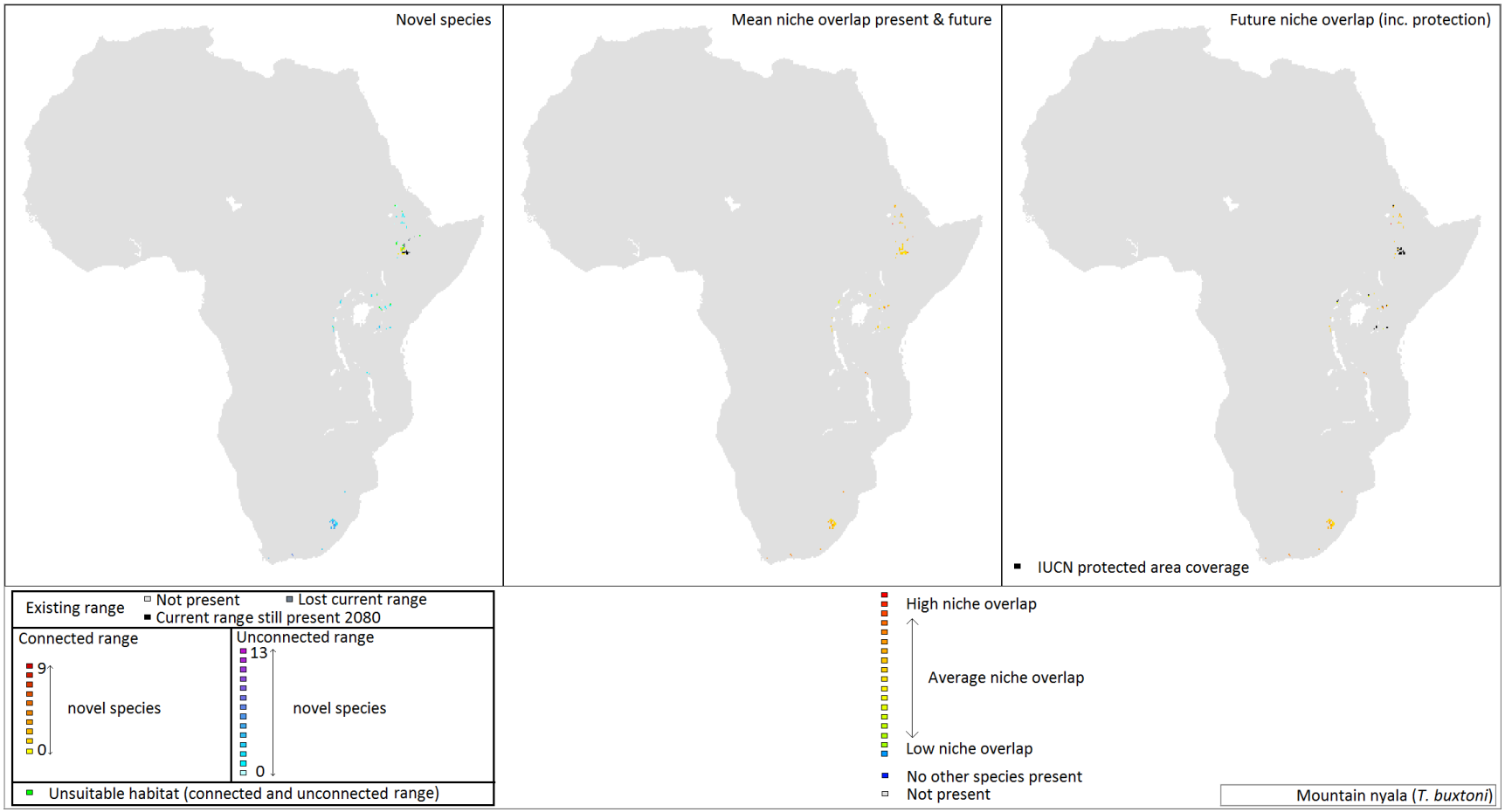

Figure 6-15: Ensemble projected range (A1B) for mountain nyala. Left: the 'existing range' retained and lost (pessimistic approach), 'connected range' (envelope approach) including areas where novel species are encountered, and 'unconnected range' similarly with novel species highlighted where appropriate. Centre: the mean niche overlap for all areas including existing areas for comparison. Dark blue signifies areas where the target species is the only one present. Right: as with the centre, but without lost existing range areas and with IUCN PAs highlighted.

Discussion

Based on the IUCN criteria for defining threatened species (criteria A3 and B2), the models in this study suggest 11 of Africa's antelope species should be classified as threatened due to climate change. A further three species (five in total) may be considered at risk due to a lack of protection in their projected ranges. This represents 19.1% of the species assessed, and includes two species predicted to go extinct if no remedial action takes place. Eleven of the 14 are already considered threatened therefore CC is added to the plight of those species. Based on these data there is an urgent need to identify conservation mitigation options that take into account the level of protection in different areas and the species' dispersal ability.

The results in this chapter highlight the question of what constitutes a species' indigenous range. The IUCN guidelines require the translocation destination site to be climatically suitable based on climate envelope models as used here. The areas must be suitable both at time of translocation and into the future, long enough to "achieve the desired conservation benefit" (Annex 5.4 IUCN/SSC, 2013). The area should also be part of that species' indigenous range referring to historical and previous areas where that species was present (see Box 6-1). This causes a problem when selecting translocation sites where a species' range is drastically altered due to climate change. The problem relates to a mismatch where indigenous range and future range may not overlap. Indigenous areas are no longer climatically suitable, and areas that are climatically suitable are not currently classified as indigenous.

> "The indigenous range of a species is the known or inferred distribution generated from historical (written or verbal) records, or physical evidence of the species' occurrence. Where direct evidence is inadequate to confirm previous occupancy, the existence of suitable habitat within ecologically appropriate proximity to proven range may be taken as adequate evidence of previous occupation."

Box 6-1: Indigenous range definition (IUCN/SSC, 2013).

Under the IUCN guidelines, areas that in the future are climatically suitable and connected to the current range are considered introductions through assisted colonization and deemed undesirable. However, if the species were able to freely disperse these areas will, over time, become recognized as indigenous. The connected cells (i.e. climatically suitable areas connected to the existing distribution through time) presented here provide an indication of these areas and therefore a species' potential indigenous range. I propose that a new

definition be adopted where 'projected indigenous range' is acknowledged as more suitable for translocation than other areas, and translocations to projected indigenous range would be categorized as 'assisted dispersal' (AD). Translocations to other areas, here represented by the unconnected cells, i.e. climatically suitable but not connected to the existing range, would be categorized as 'assisted colonization' (AC). To reflect this distinction, I propose that AC is redefined as 'translocations to climatically suitable areas having no connection to existing areas, nor the possibility for a species to disperse to those areas, through time'. For this study the assumption is that current distribution roughly represents indigenous range. Given these definitions Table 6-10 provides a ranking for potential translocation sites based on whether a species is 'stable indigenous' (i.e. current range that is climatically suitable at present and in the future), 'projected indigenous', or 'unconnected suitable' based on climatic conditions.

Site preference for translocation	**Range type (*classification*)**	**Conservation planning guidance for translocation in addition to those specified by the IUCN**
High	Stable indigenous (Reinforcement or Reintroduction)	Existing populations in these areas may require reinforcement to increase population viability. This may involve *ex-situ* populations where appropriate. Where species have been eradicated previously, habitat and species composition may have altered and present challenges to reintroduction.
Medium-high	Projected indigenous (*Assisted dispersal*)	These areas may not currently be suitable, therefore protection of existing populations or *ex-situ* conservation may be required. Potential for interspecific competition and displacement.
Medium-low	Unconnected suitable (*Assisted colonization*)	These areas may not currently be suitable, therefore protection of existing populations or *ex-situ* conservation may be required. Potential for invasive species disruption, interspecific competition, and displacement. Displacement of indigenous species should be protected against.
Low	Indigenous & unsuitable in the future (*Reinforcement or Reintroduction*)	No need for translocation as already present in these areas, however, they are not viable long term. Where species are unable to disperse naturally to areas with suitable climate, acknowledge the potential need for future *assisted dispersals/colonizations* due to changing climate/habitat. These populations may also be candidates as founder members for *ex-situ* populations, or for translocation projects, where natural dispersal in prohibited.

Table 6-10: Site preference based on the available range types. Planning guidance is in addition to existing IUCN guidelines.

Table 6-10 places stable indigenous areas as the preferred option for protection of the species. In these areas there may still be a requirement for translocations if populations in

those areas have been impacted by human activity such as hunting. This constitutes "population reinforcement" and aims to enhance population viability through increased (a) population size, (b) genetic diversity, or (c) representation of specific demographic groups or stages (IUCN/SSC, 2013).

The medium-high preference sites represent the areas that are, or will become, climatically suitable, but are not currently indigenous. These areas provide options for long term protection of species. However, the suitable areas for 2080 may not be climatically suitable at present. It is possible for them to be currently climatically suitable, but unoccupied due to habitat degradation, or localized extinction through overexploitation. If such areas can be identified and restored, these would be preferred in line with the 'high' site preference.

The medium-low preference sites have unconnected suitable areas which are climatically suitable but would not be populated by the species due to lack of connectivity. These areas are required for hirola and Aders' duiker according to the models presented here and may be far removed from the species' indigenous range. A translocation to these areas brings with it the potential risk of invasive behaviour (Mueller & Helmann, 2008) and ecosystem disruption through interspecific competition and displacement (Ricciardi & Simberloff, 2009). For the 14 species considered here, the number of novel species encountered is higher in unconnected suitable areas than in projected indigenous areas which suggests a potential for greater competition (Table 6-7 where connected cells represent projected indigenous areas, and unconnected cells represent unconnected suitable areas). Competition could also occur in projected indigenous areas where novel species are present. Careful assessment of the foraging behaviour of each resident species and the niche overlap between species before deciding on translocation sites would reduce the chances of such competition.

Finally, the low preference sites relate to existing sites that will become unsuitable in the future. According to the models presented here, these indigenous areas are not desirable for translocation. These areas become climatically unsuitable over time leading to localized extinction although species may disperse. If species are unable to disperse naturally these areas may, however, be important while translocation sites are prepared. The projections in this study indicate suitable areas in 2080; hence a potential problem is that translocation sites identified outside of the species' current range may not have a suitable climate until the end of the century. Therefore existing indigenous areas would need to be maintained until the translocation site was (a) established for conservation management; and (b)

climatically suitable. Therefore species may be required to stay in climatically unsuitable areas until a viable translocation site is ready. This being the case, management of species may be required either in current areas or in the translocation site if they are moved when the climate is not suitable. Conceivably this would include the provision of shelter, food, and water. However, if species were able to disperse and able to track climate changes as most antelopes have the potential to, then these management requirements would not be necessary (however, see chapter four where Aders' duiker is a notable exception; also see Schloss, *et al*., 2012).

Site selection process

Invasive ungulates are causing conservation problems in ecosystems globally. They not only impact directly on the vegetation on which they forage (Beltran *et al.*, 2014; Caughley, 1970), but also various aspects of the wider ecosystem including plant community structure, soil composition (Beltran *et al.*, 2014; Kardol *et al.*, 2014), interspecific competition, and displacement of native species (Acevedo *et al.*, 2010; Iriarte *et al.*, 2005). This is a concern when translocation of species to projected indigenous or unconnected suitable areas are proposed, i.e. introductions under IUCN guidelines (IUCN/SSC, 2013). However, when few or no indigenous areas remain, such alternative options may have to be considered.

There are significantly more novel species in unconnected than connected areas. This is expected as projected indigenous areas are typically found closer to the current range. Reduced risk of interspecific competition due to lower numbers of novel species therefore favours the connected areas as potential areas for translocation via AD. Even with more novel species in unconnected areas, there was no difference in the mean niche overlap between projected indigenous and unconnected suitable areas across all species. Individual species exhibit significant differences between area types, but there was no consensus on which typically was higher. This suggests that no general choice can be made between the two types of area. It is therefore wiser to simply select those areas with lower niche overlap within connected areas where possible.

Selecting areas that are projected indigenous may appear the logical choice for species translocation where required, but additional factors need to be considered as species face many other threats, largely human related (UNEP, 2010; Wilson, 1989). All species face similar threats such as habitat loss, invasive species, pollution, and overexploitation (Wilcove *et al.*, 1998). In Africa the exploitation of mammals, particularly ungulates and rodents in the tropics, reaches levels far above those found in similar areas in the Amazon (Fa & Brown,

2009; Fa *et al.*, 2002). Such levels of extraction, where there is little understanding of sustainable harvesting, present a severe localized extinction threat (Fa & Brown, 2009). Given these levels of exploitation, particularly of ungulate species, any translocation should target areas with effective protection to ensure the futures of those animals (IUCN PAs highlighted in rightmost images of Figure 6-2 to Figure 6-14).

Table 6-11 suggests suitability ranking for areas based on the factors considered in this study (cell type, level of protection, niche overlap, and novel species encountered). The table follows the logic from Table 6-10, but includes preference for protected areas with lower mean niche overlap and fewer novel species present. Retaining species in stable areas without current protection is preferred to translocation (suitability rank 1[1]) based on the fact that it reduces the threats posed by invasive species, competition, and displacement caused through translocation.

Stable (**S**) indigenous, Connected (**C**), or Unconnected (**U**) cells with suitable habitat in 2080	IUCN Protection (**Y**es/**N**o)	Mean niche overlap in future range compared with current range. Areas with higher niche overlap signifies similar dietary requirements. Within each category the areas with the fewest novel species would be preferred.		Suitability Rank
		NA	Not applicable (current/stable cells)	
		Z	No overlap (no other species present)	
		L	Lower/Average mean niche overlap	
		H	Higher mean niche overlap	
S	Y	NA		1
S	N	NA		1[1]
C	Y	Z		2
C	Y	L		3
C	Y	H		4
U	Y	Z		5
U	Y	L		6
U	Y	H		7
C	N	Z		8
C	N	L		9
C	N	H		10
U	N	Z		11
U	N	L		12
U	N	H		13

Table 6-11: Priority ranking of areas where species should be protected, or translocated for protection, based on protection coverage, mean niche overlap, and number of novel species. Stable indigenous cells represent existing range after contraction due to climate change, connected cells are projected indigenous areas appropriate for AD, and 'unconnected' are unconnected suitable areas available for AC. [1] Highly recommend the PAN be extended to these areas.

There are many other considerations when selecting a translocation site. For example, the distance to the species' existing range. Though not guaranteed, nearer areas are likely to

have more similar composition of vegetation to those found in the species' current range. The projected indigenous areas tend to be closer to the existing range so this is partly accounted for under the selection process described. Vegetation also tracks climate change although it may not keep pace with those changes (Corlett & Westcott, 2013). Therefore minimising the translocation distance between current and future range would provide greater chance for vegetation to be naturally present. However, herbivores play a vital role in seed dispersal (Pakeman, 2001). Therefore, if antelopes are limited in their dispersal, it follows that the dispersal of plants will be affected too. The above is not meant to represent an exhaustive set of criteria. It acts as a framework to roughly rank areas according to their potential before assessing those sites individually.

Species analysis and recommendations

Below I discuss in more detail the 14 species threatened by CC, either individually or in groups displaying similar attributes or range predictions. These provide a first step in the identification of suitable areas for potential translocation. These areas then require refinement and individual site assessment to ensure that both suitable habitat and resources for the translocated species are present and that the risk of detrimental impact on existing ecosystems and species is minimal.

Sahel & Sahara

Both the addax and dama gazelle are already critically endangered due to habitat loss, domestic livestock mismanagement, and hunting. They are considered to be the Saharan bovid species most at risk (Newby & Wacher, 2008; Newby *et al.*, 2008). The addax loses its existing range, while the dama gazelle has its range reduced to 36 cells or an AOO of 1,947 km^2 (Table 6-4). If judged on CC alone, the dama gazelle would be classified vulnerable due to small range (IUCN criteria B2), and endangered through the projected reduction in population (IUCN criteria A3; Table 6-5). This is a grave concern because dama gazelle's threat status is already CR. Remaining populations are at threat from under resourced protected areas (Newby & Wacher, 2008) and destabilization of conservation efforts due to military unrest (Newby *et al.*, 2008). These threats suggest both species should be assessed for possible translocation sites.

The addax has 401 connected cells with suitable conditions if dispersal is unlimited. If dispersal is hindered, these areas provide opportunity for AD including 54 cells providing protection by IUCN. The results highlight Aïr de Ténéré national reserve in Niger as a large important area providing protection to both addax and dama gazelle. The two species

currently have overlapping ranges with differing dietary requirements. Addax are variable grazers with 80% grass in its diet compared with the browser/grazer diet (47.5% grass, 47.5% browse) of the dama gazelle (Gagnon & Chew, 2000). This suggests, given adequate resources, the two species can continue to coexist successfully.

Aïr de Ténéré national reserve includes an IUCN category Ia reserve (strict control on human visitation and usage) designated "Addax sanctuary". IUCN records suggest the species was present in this area in the past (Newby & Wacher, 2008) suggesting it is a suitable candidate for translocation projects for the future given continuing suitable climate. However, Aïr de Ténéré national reserve presents cause for concern related to military unrest (Newby *et al.*, 2008). Whether this continues is unclear, beyond this area both species have overlapping future ranges with protection in Algeria. It also demonstrates that even the highest profile national reserves require adequate protection to protect the species therein.

Further west on the border of Western Sahara and Mauritania a strip of connected cells provide suitable conditions with no novel species, but without protection. This may provide an alternative for both species should the current protected areas remain unstable. There are more areas with suitable conditions for both species to the east of their existing range. These are combinations of connected areas for the dama gazelle and unconnected areas for the addax. However, both species historic range includes areas to the west and therefore these should be considered before non-native areas (IUCN/SSC, 2013).

Both species are subject to breeding programs in captivity and reintroduction programs (Stanley Price, in press; Newby & Wacher, 2008; Newby, *et al*., 2008). With both species having limited wild populations, and facing existing and new threats, these *ex-situ* efforts should continue. Reintroduction efforts should consider the data provided here to ensure continuity of suitable areas into the future.

Hirola

The hirola is already critically endangered due to drought, disease, livestock competition, and habitat loss. Populations have declined 85-90% post 1980 with the Somalia population probably already lost (IUCN SSC Antelope Specialist Group, 2008a). Current estimates suggest 350-500 individuals remain (Probert *et al.*, 2014). The continuing impact of climate change on this species suggests no connected areas in the future even if the species were able to disperse. This leaves the option of assisted colonization (AC). Such an introduction has taken place with some success in Tsavo East National Park, Kenya. The population

originally grew (Andanje & Ottichilo, 1999), but has now remained stable at approximately 75 since 2000 (Probert *et al.*, 2014). This may be related to the hirola's dependence on habitat (short, green grass during the summer) and it is unclear if they are able to utilize "marginal" habitat (Probert *et al.*, 2014). This highlights the need for further detailed assessment of the species' yearly foraging requirements. The relocation sites would then need to be assessed to establish suitability. The introduced Kenyan population is also located in an area suggested to be outside the species' climatic window for 2080 based on the results above.

With only 30 unconnected cells providing suitable conditions for hirola in 2080, the nearest areas to the current population that are suitable and protected are in southern Ethiopia. Five cells have existing protection via an IUCN PA (Borana controlled hunting area); however, these have more novel species and greater niche overlap than the areas to the west of Africa in Angola. The Ethiopian option potentially offers similar foraging options compared with the distant Angolan areas.

With limited *in-situ* options available for the hirola, other conservation strategies need to be considered such as establishing an *ex-situ* population in suitable conservation centres. The problem with such strategies is the need to remove a significant percentage of the *in-situ* population to establish a genetically viable breeding program.

Duikers

There are 18 members of the Cephalophini tribe of duikers found in Africa. Typically forest dwelling species, all but the grey duiker (Sylvicapra grimmia) are specialist fruit eaters (Gagnon & Chew, 2000). It is common for duiker species ranges to overlap across Africa. Table 6-8 details the five species of duiker (Aders', Peters', Jentink's, white-bellied, and Abbott's) that are either threatened by CC or lack protection. Note that while most of the species are considered here, the Abbott's duiker is considered below in the Montane/Highland species section.

Aders' duiker is at risk due to CC as it is predicted to have no climatically suitable stable range or any climatically suitable connected range, and therefore would rely upon unconnected areas for protection. Aders' duiker is currently found on the island of Zanzibar and in two areas on the coast of mainland Africa. The lack of connected future areas is due to habitat conversion from forest to grassland that surrounds its current distribution, the last stand of Arabuko-Sokoke forest, Kenya (Finnie, 2008). This lack of connectedness due to habitat

conversion results in nearby areas being categorized as unconnected. However, if the nearby habitat was pristine then those nearby areas would be categorized connected, and therefore the preferred option.

There are large areas of suitable habitat located both on the coast and inland, ranging from the east to the west of the continent. These areas contain large protected areas and therefore options for translocation are present. When selecting an area and considering competition and niche overlap, all but one cell provide higher niche overlap than at present. This is due to a low overlap in current areas which is caused by it being the only antelope species on Zanzibar and there being low overlap in the remaining cells. Therefore areas with lower levels of niche overlap and fewer novel species would be preferable. Similarly, areas close to the species' current distribution are likely to provide similar species of vegetation for foraging. This presents Selous Game Reserve (GR) in Tanzania as the closest large protected area. No novel species are present suggesting that coexistence is likely to be possible.

Aders' duiker in the east of Africa has a similar climatic envelope to that of the Jentink's duiker in the west of Africa, although the Jentink's duiker has a somewhat wider envelope. Both duiker species unconnected ranges demonstrate large areas of overlap. Jentink's duiker retains 145 cells of its existing range in 2080, but has no protection in Liberia and Sierra Leone. The preferred option would be to provide protection in the species' stable indigenous area as large areas remain climatically suitable. However, if development of PAs was impossible in the indigenous area, the species may rely on unconnected areas that provide IUCN PA protection across central Africa. There are PAs present in northern DRC with relatively low numbers of novel species and low niche overlap that would reduce risk. Selous GR in Tanzania is also suitable but further removed from the species' current distribution. It may also introduce unwanted competition to the Aders' duiker if that were to be translocated also.

As with the Aders' and Jentink's duikers, Peters' and the white-bellied duiker share a similar climate envelope. The white-bellied duiker has a wider existing distribution with the two species ranges overlapping significantly in the west of the white-bellied duiker's range. In 2080 both species will be considered vulnerable due to projected range contraction; however, both species are afforded protection in their existing ranges and therefore these may be at lower risk of extinction than several other species considered here. Still, from a conservation perspective, they are species to be aware of and the present study shows that

alternative areas for translocation are available should they be required. For example, given their co-existence, Peters' duiker could be subject to AC into the reserves in the east of DRC where the white-bellied duiker are present: there are no novel species, and similar levels of niche overlap exist.

Somalian species

Somalia continues to be politically unstable and conservation efforts within the country are likely to be unfeasible. There is no central government control, a prevalence of weapons, over-exploitation of bushmeat, and a lack of protected areas (IUCN SSC Antelope Specialist Group, 2014). Four species are largely endemic to Somalia and are projected to be threatened due to lack of protection. Two species are considered threatened due to lack of protection alone (Speke's gazelle and beira), while dibatag and silver dik-dik also have small ranges. None of the species lose their range completely albeit the ranges of the dibatag and silver dik-dik are greatly reduced (Table 6-6). Speke's gazelle has the most modest percentage reduction in range of the 14 species and it retains a range of 377 cells. However, the future of the species in such an unstable country, where no protection exists and conducting surveys is challenging, must be considered at risk.

The silver dik-dik presents serious cause for concern from a CC perspective. Its existing range is reduced to a thin strip with suitable conditions in Somalia. Additional connected areas suitable for AD are present in Somalia only. Beyond Somalia only 19 fragmented cells are available, with one cell providing protection. A cluster of cells, without protection, are available in Angola. Unless additional protection can be provided, silver dik-dik need to be considered as a candidate for *ex-situ* conservation as suggested previously by East (1999). A similar situation applies to the dibatag. Only five Somalian cells remain of its existing range, but large expanses of Somalia provide suitable conditions. As with the other Somalian species, AC of more remote areas needs to be considered to protect the dibatag in a more politically stable environment. Beyond Somalia there are 62 unconnected cells grouped in Angola and Namibia, Senegal and Mauritania, and a single cell in Eritrea. The Senegal and Mauritania areas are predicted to be free of all antelopes in 2080 but they are currently unprotected. The Angola and Namibia cells are fragmented but one offers IUCN protection in Dombe Grande reserve. This cell is also the single protected area available for the silver dik-dik and therefore could be considered as a destination for a dual AC. Dombe Grange reserve would, however, present high niche overlap with other species for both silver dik-dik and dibatag. In addition both silver dik-dik and dibatag have the same composition of diet

(80% browse, 10% grass, and 10% fruit). While the dik-dik is smaller than the dibatag this does not ensure browsing exclusivity at different heights (du Toit, 1990) and therefore competition could affect the species, especially the dik-dik. On the other hand, these two species currently have overlapping ranges (IUCN, 2011), and the fact that many browsing species overlap ranges in other areas suggests this is not a limiting factor. It would still be prudent, if possible, to gather more data on the ecological needs of both species. As with the silver dik-dik, *ex-situ* conservation efforts may be required to ensure the long-term survival of the dibatag. With a small dibatag population still remaining in Ethiopia (Wilhelmi *et al.*, 2006) there is an opportunity to utilize these animals as founding members if the removal of those individuals does not endanger the wild population.

Compared to the dibatag and silver dik-dik, the beira and Speke's gazelle have more areas with suitable conditions and habitat available to them, including connected areas in Somalia, that would be climatically suitable for AD. However, with the political instability in the country alternative options would be required. Eastern Ethiopia offers potential areas for both, but currently there are few protected areas in the east of the country (United Nations Environment Programme World Conservation Monitoring Centre, 2010). Beyond the connected areas there are potential AC areas for beira and Speke's gazelle near coasts around the continent including areas where no other antelope species are predicted present. These antelope free areas include protected areas in southern Namibia suitable for both species. Such areas present the opportunity to translocate and protect both species in areas with reduced interspecific competition. Beira and Speke's gazelle differ in diet composition with beira being a browser (90% browse) and Speke's gazelle a mixed feeder (50% grass, 50% browse) (Gagnon & Chew, 2000) therefore competition between these species is expected to be weak. Other opportunities for AC of protected areas are in fragmented areas around the continent. The larger area in Namibia may offer the best option for both species particularly in terms of future population expansion.

Montane/Highland species

The mountain nyala is already categorized endangered due to a small population, hunting, and habitat loss (Sillero-Zubrili, 2008). Under CC mountain nyala experience a contraction of range that would also set its threat status to EN due to a small AOO under IUCN criteria B2 (Table 6-4). All cells within the 2080 range are protected. Nine cells within the existing range remain climatically suitable until 2080; this is a 33% reduction in range. There are eight nearby connected cells in Ethiopia that present suitable conditions and protection where

populations could be established to provide protection from localized stochastic events such as disease, fire, and pests (Beazley, 1997). This would present opportunities to boost the population from the current estimate of approximately 3,750 (Atickem *et al.*, 2011). Despite being protected mountain nyala continue to suffer from poaching in areas with ineffective patrols (Atickem *et al.*, 2011). This must also be addressed if the existing population is to remain secure. Beyond Ethiopia, there are fragmented cells in Kenya, Tanzania, and DRC that are predicted to provide suitable climate. These are small areas that overlap with the Abbott's duiker's habitat (see below). The mountain nyala is typically found at high elevations between 1,750-3,400m (Atickem *et al.*, 2011; Sillero-Zubrili, 2008) characterized by cooler temperatures. Although the Abbott's duiker has a wider climatic envelope than the mountain nyala, they overlap in these cooler areas. Lesotho to the south of Africa also provides suitable climate given its high elevation. However, there are currently no IUCN protected areas in Lesotho. Mountain nyala would encounter up to eight novel species in Lesotho, although the niche overlap index is similar to that which they currently experience. Given the availability of closer areas with protection, these would be likely to take priority.

Abbott's duiker is threatened by a contraction of range to eight cells. Currently endangered, Abbott's duiker has a fragmented range in the montane and submontane forests of Tanzania (Bowkett *et al.*, 2014; Moyer *et al.*, 2008). Five of the eight cells provide protection in the future, however, the limited distribution of the species is the reason it is considered here. Connected and unconnected cells are available for AD and AC if the species were to have its range expanded. The connected cells are all in Tanzania but only one offers protection; unconnected cells are present in Tanzania, Kenya, Ethiopia, Rwanda, DRC, and Burundi. The largest areas of protection, and lowest levels of novel species and niche overlap, are found in Ethiopia centred on the Bale Mountains where mountain nyala would be a novel species.

Abbott's duiker and mountain nyala are species that suffer from fragmented distributions caused partially by their need for cooler temperatures driven by high elevation, but also human pressures. Globally hotter temperatures caused by CC can force species to higher elevations, thereby reducing potential range (Moritz *et al.*, 2008). The Abbott's duiker shares a similar climatic niche with mountain nyala but are found in warmer areas as well. If the mountain nyala moves to higher elevations within its existing range, as predicted, it may be possible to translocate the Abbott's duiker to the areas vacated by the nyala. There are no other novel species suggesting they could co-exist. However, as with all assisted colonizations, careful consideration and evaluation of potential interactions with other

species are required. In addition, if the Abbott's duiker were translocated to lower elevations, previously occupied by mountain nyala, they would be expected to naturally disperse to the mountain nyala's new range over time. This would then require monitoring for any effect of competition. Weak foraging competition between the species is expected as the Abbott's duiker has a largely fruit diet (71%) compared with the mountain nyala's mainly browse diet (70%).

Nile lechwe

The endangered Nile lechwe is predicted to require AD or AC. The species' current range is rendered unsuitable in both South Sudan and Ethiopia. There is a small area available for AD within connected cells; two of the 15 cells offer fragmented protection in the south of South Sudan, and in Uganda along the border with Kenya. Larger unconnected areas are present in Ethiopia and Kenya, both with protection available. While large areas are available, the ecology of this species is especially important to consider. Nile lechwe require wetlands and are often found in shallow water (10-40cm) on the edge of deep swamps (IUCN SSC Antelope Specialist Group, 2008b). They have adaptations such as splayed, elongated hooves, evolved to ease movement in muddy areas (Kingdon *et al.*, 2013). They are also protected from typical antelope predators such as lions and leopards (*Panthera pardus*) by the swamps they inhabit and enter deep water when disturbed (Kingdon *et al.*, 2013). Without this option for protection, the species may be at greater risk and therefore selection of future areas would require similar conditions. The Nile lechwe highlights the importance of considering autecology when searching for possible translocation sites. While it is possible that species will be able to adapt to new species of vegetation provided there is sufficient quantity of its preferred type, other elements of their habitat may not be equally replaceable. This emphasizes the need to incorporate detailed ecology and behaviour traits of the species when selecting translocation sites. The areas available for AD have no major rivers running through them with the Nile being to the west of the predicted future range. The potential AC range includes areas along the Tana and Galana rivers and Lake Baringo in Kenya, and areas bordering Lake Malawi, in Malawi. Hence, while this study can identify areas that are broadly suitable in terms of climate, habitat, and low risk of interspecific competition, individual sites need to be assessed in detail, particularly for species with a highly specialized niche such as the Nile lechwe.

There is a growing captive population of Nile lechwe (IUCN SSC Antelope Specialist Group, 2008b; Falchetti & Mostacci, 1993) which, given the uncertainity for the wild population should be maintained.

Prioritizing species

The cost of translocation is high (Kleiman, 1989) and funding projects for every species in this study is unlikely to be financially viable. Based on the criteria and results above, it could be argued that highest priority should be afforded to those species that are predicted to lose their current range and without any connected range in the future (hirola and Aders' duiker). These may be followed by those losing their current range, but with connected range (addax and Nile lechwe). I suggest that, due to the increasing threat from humans, those species with no-protection should be considered next. This includes all of the exclusively Somalian species (dibatag, silver dik-dik, beira, Speke's gazelle, as well as Jentink's duiker). Jentink's duiker may, however, be protected in its current range if PAs were established whereas this seems unlikely for the Somalian species. The five remaining species (Abbott's duiker, Peter's duiker, white-bellied duiker, dama gazelle, and mountain nyala) have, within their range, protected area coverage that remains in the future. Based only on the threat from climate change, these would therefore be considered the lowest priority of the 14 species.

With the high costs it is preferable to combine translocations to particular sites. This was highlighted above for the silver dik-dik and dibatag, and the beira and Speke's gazelle. In these cases, if there is low chance of competition between the existing species, and those being translocated, a dual-translocation would potentially reduce costs of monitoring and management (fencing and wardens).

Single species areas

Introducing a species to an area where there are no other antelope species may seem intuitive as there will be reduced competition for resources (although other ungulate and herbivore species are likely to be present). Some of the species discussed above present this opportunity, but there are very few protected areas within those zones. Whether natural predators would be present is unclear, but if absent placing species in those areas might be likened to *ex-situ* captive populations. This would be similar to other African antelope reintroduction projects which remain fenced populations (Stanley Price, in press; IUCN SSC Antelope Specialist Group, 2013). However, if these are to be the final destination for those species then other considerations are required. Firstly, an area with a single antelope species and few predators, is likely to present limited nature-tourism opportunities. Such tourism

may be key to conservation efforts. Typically visitors to Africa want to see large mammals with emphasis on the big cats, elephants, and giraffe (Goodwin & Leader-Williams, 2000), potentially limiting the appeal of areas without them. Attempts at elevating a species to flagship status has proven successful in raising the appeal of areas to attract tourists, but they also act to engender local support for conservation through benefits received from tourism (Walpole & Leader-Williams, 2002). This might be particularly true if it is one of the few remaining places to see that species. Local support for projects is important to their success (van der Duim & Caalders, 2002; Dunham, 2001). However, it is questionable whether 'non-native' species are suited as flagship species and will be embraced by local communities.

Ensuring success

Despite careful planning there are inevitably threats that face translocation projects. Reviewing reports on both successful and unsuccessful projects may help deliver future success. Project successes involving ungulates point to the importance of sufficient funds to "obtain and release significant numbers of animals" (Swanepoel & Dunham, 2013) where "relocations" of groups >100 have higher success rates (Fisher & Lindenmayer, 2000). Other factor contributing to successful projects include: (i) large areas for species to be released into (Swanepoel & Dunham, 2013; Zhigang, 2013); (ii) public awareness programs highlighting the importance of species (Shah *et al.*, 2013); (iii) encouraging flagship status with local government backing for veterinarians and wardens; and (iv) prior scientific research into ecology, behaviour, reproduction, genetics, and disease prevention (Zhigang, 2013).

Even with prior scientific research it may not be possible to guarantee complete success. Interactions with other species, particularly predators, may be important to establishing self-sustaining populations. Clegg *et al*. (2013) found that low density antelope species such as Lichtenstein's hartebeest (*Alcelaphus buselaphus* ssp*. lichtensteinii*) suffer in areas of high lion density, although other antelope densities were not reported. There is also the potential for behavioural changes in isolated populations. In particular, any loss of anti-predator behaviour in the absence of predators (Blumstein & Daniel, 2005) could have consequences when contact is re-established (Berger *et al.*, 2001; Gittleman & Gompper, 2001).

The importance of post release monitoring and incorporating local people into the management plan cannot be overlooked. Dunham (2001) found that there is a need to monitor, and understand the reasons, for population fluctuations particularly where feral

dogs may be a problem. Dunham describes a project where mountain gazelles were reintroduced onto the Hawtah reserve in central Arabia. Fences were erected on the reserve to stop the local population visiting certain areas. This was done without local consultation. The fence was subsequently destroyed and this is linked with the start of a poaching problem that saw the population of mountain gazelle decline rapidly. This was compounded by a lack of law enforcement whereby rangers protecting gazelles had no legal powers to arrest (Dunham, 2001). The example highlights that, in translocation sites where poaching is unavoidable, there is a need to establish proper law enforcement. Fences within and around protected areas are typically driven by a need to protect against the transmission of disease, largely from livestock, and to reduce poaching and crop raiding (Lindsey *et al.*, 2013; Lindsey *et al.*, 2009; Newmark, 2008). However, opening borders of reserves can have many benefits such as (a) allowing dispersal and migration, (b) offering ecological resilience to localized drought, fire, and flood, as well as encouraging larger populations, and (c) providing access to varied habitat types, allowing complete fauna assemblages (Lindsey *et al.*, 2009). Such benefits rely on support from surrounding land owners. It is important to recognize that local views and objectives may alter over time as a consequence of changes in land ownership or political changes. The need for long term protection is also important as the presence of wildlife in reserves attracts poachers (Swanepoel & Dunham, 2013). If the translocation guidelines are followed, and previous project experience is considered, the hope is that future translocations will succeed.

Antelope translocations should also consider any potential for genetic dilution through hybridization. This may be of potential concern for relatively young species such as many of the duikers (Johnston & Anthony, 2012; Fernández & Vrba, 2005) where hybridization between existing sympatric species may still continue in the wild (Johnston & Anthony, 2012). Hybridization has also occurred in zoos between similar species such as those in the tragelaphine tribe (Antelope Taxon Advisory Group, 2013). The number of individuals, and the demographic breakdown of those individuals, is also of importance. Minimum populations of 50-100 individuals has been suggested for a range of African ungulates (Swanepoel & Dunham, 2013) with over 30 adults of breeding age being recommended for rapid population growth in Lichtenstein's hartebeest (Clegg *et al.*, 2013).

Habitat suitability

This study utilizes a habitat filter to restrict specialist foragers from entering unfavourable habitat therefore restricting certain areas. It is a static filter that assumes no change in open

and closed areas over time. As mentioned in the methodology (see 2.7), this approach was adopted due to (i) the considerable time lag expected before an area will switch from one habitat to another (Corlett & Westcott, 2013), and (ii) the lack of continental scale vegetation forecasts based on climate change. I acknowledge that this is a simplification of the actual suitability of habitats for particular species. A finer habitat filter would allow more refined maps of species specific vegetation suitability to be developed. This may be possible in the future as finer scale continental projections become available.

Conclusion

This study highlights those 14 species most at threat either due to climate change or through a lack of protection through the Africa's IUCN protected area network. All species have areas presenting suitable climate in the future, but two only have unconnected areas and are thus forecast to require assisted colonization. Four more species have no protected areas in their current and projected indigenous ranges. Three further species have very limited areas with protection (under 5 cells) within those same areas. This will likely result in the need to utilize the protected areas in unconnected areas if funding cannot be found to develop new protected areas in the existing or projected indigenous range. Unconnected areas bring greater uncertainty due to the presence of more novel species and the potential for interspecific competition, especially where species may act invasively. This particularly affects the four species centred in Somalia and raises the profile of civil unrest as a threat to species in Africa. The status of Somalian populations is unclear (IUCN, 2014a) and gaining access to those animals to form part of a translocation would likely entail many risks to humans, animals, and thus the success of the project.

The present findings show that climate change has the potential to reduce species' range to the point of extinction, especially where dispersal ability is limited and formal protection is absent; this threat is compounded by the likely changes in land use and increases in exploitation driven by human population growth. However, Africa is the second largest continent and has areas of suitable climate and protection for all of its antelopes, albeit limited for some. Given sufficient resources and adequate protection there is an opportunity to ensure that all species persist.

7. General discussion

This PhD thesis demonstrates that climate change poses a significant threat to many antelope species in the future. Below I review the main findings of this study in the context of concerns for antelope conservation over the 21st century, I take a critical view of the modelling process, and make suggestions as to where improvements could be developed.

General findings

Chapter three aimed at clarifying patterns linking species ecological and morphological traits with their climatic preferences. The results showed that the selective diet was linked to a narrow temperature range, a finding mainly driven by the specialist forest antelopes. Also, species with preferences for wider temperature ranges were found to be associated with larger body mass and higher percentage of grass in the diet. However, the scarcity of the significant ecological and morphological predictors of climate preferences suggests that a rich diversity of ecological niches exists under most climatic conditions, which agrees with the great diversity within the antelopes. Hence the general findings highlight the species heterogeneity across the wide range of Africa's climates.

Chapter four indicated that threatened species are disproportionately affected by climate change as they experience relatively greater range contraction under both envelope and pessimistic approaches. Irrespective of the climate model or climate scenario, by 2080 the critically endangered hirola is predicted to have no range remaining and no suitable areas in which to disperse. Based on the envelope approach most other species exhibit range contraction rather than expansion and some of these are drastic. Considering the general rise in projected global temperatures those species with preferences for warmer conditions performed better. By using the three modelling approaches it was possible to explore different potential futures for Africa's antelopes:

> *Envelope approach*. The aim of the envelope approach was to identify areas of climatic suitability for each species and to investigate whether there were general trends in terms of gains or losses. This represents a niche model that identifies potential habitats for species, but does not consider restrictions imposed by limitations on dispersal ability (Araújo & Guisan, 2006). The results demonstrate that over 80% of species will experience a reduction in suitable habitat. Antelope species present a diverse group of varying morphology, ecology, and behaviour, and the attribution of range contraction to temperature rises rather than changing

precipitation patterns or other species traits may suggest a more general pattern for other taxonomic groups particularly mammals.

Pessimistic approach. With the predicted quadrupling of human population in Africa by 2100 (United Nations, 2014), and the existing pressures placed on antelope species and the ecosystems upon which they rely, the assumption of the pessimistic approach, that antelopes cannot disperse, may be valid and present the likeliest future. Recent habitat projections suggest widespread conversion of natural habitat across Africa over the next few decades (van Asselen & Verburg, 2013). This will reduce suitable habitat and may place greater importance on the need to ensure species are protected within the protected area network. Populations outside of protected areas typically perform worse than those inside (Geldmann *et al.*, 2013) suggesting that protected areas may become the only areas where viable populations can persist. Further analysis of the results from the pessimistic approach in chapter six identified 14 species as threatened due to climate change or due to lack of protection.

Optimistic approach. A common criticism of species distribution models and similar methods is the absence of dispersal ability for species within the predictive models. Here, the optimistic approach extended the standard environment niche model with the spatial restrictions of a generalized dispersal ability (Araújo & Guisan, 2006) to investigate how species would disperse from their current range at a species-specific dispersal velocity. The results in chapter four identified that over half the species would see range expansion compared with their existing distributions if they were allowed to disperse. However, this must be considered alongside the results from the envelope approach where over 80% of species experience a decline in suitable conditions. This indicates that species existing ranges are currently constrained by factors other than climate. This is consistent with the fact that many antelopes are known to have experienced range and/or population contraction over the past century (East, 1999) and therefore the increases in range demonstrated under the optimistic approach mainly reflects a repopulation of extirpated areas. This indicates a further serious threat to antelopes, that of human population expansion and the pressures of humanity on these species (see below).

The three approaches provide different views of the future. However, based on the multiple threats faced by antelopes and without greater protection for antelope species, both inside and outside of protected areas, the pessimistic results may present the more likely outcome.

Given the contraction of suitable conditions for many species, chapter five focused on the need to develop a protected area network and identify important conservation areas for antelopes. Both novel protected areas, and significant expansions of existing protected areas, were identified as important if we are to protect all species to the minimum requirements set out by the low and high protection scenarios presented. This would require up to 8.7% of Africa's land mass to protect antelopes in light of distribution changes brought on by climate change. As indicated above, the threat of climate change is one of many faced by antelopes. Overexploitation and subsistence hunting is unlikely to recede in the near future as the human population in Africa is forecast to quadruple by 2100. It may be that protected areas shelter the only viable wild populations in the future and may enable these to act as source populations for *in situ* conservation (Gaston *et al.*, 2008; Naranjoa & Bodmer, 2007). Thus, there is an urgent need to improve the performance of protected areas in Africa. Geldmann *et al.*'s (2013) meta-analysis found that populations of mammals, birds, insects, and their habitat typically perform better inside protected areas. However, population declines are still common inside protected areas. Craigie *et al.* (2010) also found declining populations in Africa's protected areas thus highlighting a need to improve the protection afforded by these areas.

Chapter six identified the need to re-evaluate how species are classified as threatened to reflect the threat from climate change. The IUCN methodology enables users to categorize species as threatened based on forecasts for the future, such as contraction of range (either the extent of occurrence or area of occupancy), however, there is a restriction whereby the contraction must occur within three generations or 10 years, whichever is longer (IUCN Standards and Petitions Subcommittee, 2014). Climate change is measured, and projected, over multiple decades or centuries and therefore in some cases the IUCN methodology restricts categorization of species based on climate projections (Keith *et al.*, 2013; Hannah, 2012;). Here, I extended the IUCN methodology in two ways: firstly I extrapolate range contraction for species over the century and over multiple generations to identify threatened species; and secondly I suggest that a minimum protected area coverage should be set as a requirement for heavily exploited species, such as antelopes, as populations outside protected areas may not be viable long term. Using this approach I identified 14 species that

have threat statuses assigned due to climate change and/or a lack of protected area coverage in the future. For these species I expanded the search for suitable climatic conditions beyond the areas connected to their existing range and identified areas for potential translocation. There are predicted suitable areas for all 73 species in 2080, however, for some these are limited in size and provide limited protected area coverage.

Evaluation of modelling approach

This thesis sought to address some of the criticisms faced by species distribution models and their application to predict future species ranges. Below I review the main advances in terms of modelling approach made in this study (although not exclusive to this project), and I also make suggestions for further methodological refinement:

1. Dispersal ability is often excluded or considered under an all or nothing approach in species distribution modelling or niche modelling (Araújo & Peterson, 2012; Franklin, 2010; Thuiller *et al.*, 2006). As described above, dispersal ability was incorporated into the predictions for each species, based on Schloss *et al*. (2012), under the optimistic approach. In addition, unfavourable climatic conditions were used as barriers to dispersal. Basing the dispersal velocity on body mass for all species does not take into account species specific dynamics such as natal dispersal age and social behaviour. Nor does it take into account aspects of population dynamics and behavioural ecology such as population density, resource competition, habitat quality, or a species' ability to migrate through heterogeneous landscapes (Bowler & Benton, 2005). As further species specific data become available in the future it may be possible to better refine the dispersal ability of each species. This would likely require the incorporation of the habitat filter and other biotic interactions (see below).
2. Habitat suitability was used as a filter for habitat specialists to restrict modelled dispersal through unfavourable habitat. The habitat filter had no significant impact on the results yet it may be advisable to refine the filter. The filter was based on species being broadly categorized as open, closed, or generalist species relating to their preference for savannah/grassland, forest conditions, or no preference in habitat. While the habitat filter in this thesis was used to limit dispersal, other studies have used habitat as a predictor of resource quality and therefore species distributions (Evangelista *et al.*, 2008). Therefore, in the future, it may be possible to refine a habitat filter to be included as a predictor and as a dispersal filter.

Evangelista *et al*. (2008) used remote sensing imagery (satellite vegetation indices) to correlate species distribution with vegetation type index values. However, these values are not currently projected for the future. If these vegetation indices could be reliably projected, perhaps using similar methodology to that used in this thesis, these may be used as a predictor and/or dispersal filter. Alternatively, global vegetation models continue to evolve through the development of dynamic global vegetation models (DGVMs). Sato & Ise's (2012) DGVM presents a continent-wide 0.5° x 0.5° projection for one climate scenario (A1B) and defining five biome types, while Moncrieff *et al* (2013) present 1° x 1° projections, with four vegetation types. Whether this few biome/vegetation types would improve the habitat filter is unclear. Furthermore, projections at a finer resolution, matching the climate projections, would be desirable.

3. Species distribution models are often criticized for including inappropriate predictive variables (Araújo & Guisan, 2006; Guisan & Thuiller, 2005) or too many variables resulting in multicollinearity and overfitting (Ashcroft *et al.*, 2011; Graham, 2003). The models should include the causal environmental predictors (Guisan & Thuiller, 2005), and the contribution of each variable should be assessed (Araújo & Guisan, 2006). Here, the predictive variables were carefully selected: they were highly significant predictors for most species distributions thus reducing the likelihood of spurious correlation (Ashcroft *et al.*, 2011); they had a low degree of collinearity; they had previously been identified as important to delimiting distributions (Hopcraft *et al.*, 2009; East, 1984); and they were physiologically and ecologically relevant to antelope species (Owen-Smith, 2002). The models developed for this thesis were based on climatic variables for two main reasons: (i) they proved the most reliable and best performing across a number of assessments; and (ii) the main aim of this thesis was to assess the impact of climate change on African antelopes. The clarity of the results were increased by focusing on climate variables and excluding uncertain projections in other environmental variables. In other studies, habitat and vegetation indices have been used successfully as a predictive variable of current antelope distributions (Pettorelli *et al.*, 2009; Evangelista *et al.,* 2008; Mueller *et al.*, 2007), as has soil (East, 1984), and in the future it may be possible to include additional abiotic variables; however, as noted above, this would require confidence in the projected data.

4. The human footprint filter was included to reduce the likelihood of species being present in areas of high land transformation by humans (Thuiller *et al.,* 2006). This filter was static due to a lack of future predictions, however, recent research on land-use change provides global estimates of urbanization, agricultural intensification, tree cover loss, and land system use (broad vegetation types) comparing the year 2000 to 2040 (van Asselen & Verburg, 2013). Such studies offer the potential to act as dynamic human footprint filters to replace the static methods used here. Land-use projections may become increasingly integrated into the production of climate projections (Hibbard *et al.*, 2010) as land use affects local and regional climates (Boko *et al.,* 2007; Hulme *et al.*, 2001). However, human growth and impact are difficult to predict with high confidence (Araújo *et al.*, 2008) so caution must be applied.
5. To account for inconsistencies across climate projections from different global climate models, species predictions were based on ensemble models to increase confidence in the results (Fordham *et al.*, 2011). In addition to the ensemble models produced here others have used the term 'ensemble' to address the inclusion of multiple predictive modelling techniques (Araújo & New, 2007). Under this approach, multiple species distribution models are produced for each species using different statistical modelling methods. For example, here I used generalized linear models in preference to generalized additive models, random forest, surface range envelopes, multivariate adaptive regression splines, classification tree analysis, or artificial neural networks. The selection of GLMs was primarily due to their realism in modelling ecological relationships (see Elith *et al.,* 2006; Austin, 2002;) where they contrast with several other modelling techniques. Other factors include their better performance in terms of accuracy, temporal independence (i.e. they can be applied over different time periods), ability to extrapolate beyond existing ranges (Marmion *et al.*, 2009), and their ability to easily identify optimal conditions. However, others have argued that more robust forecasts may be produced using the multiple SDM "ensemble" approach. This method produces a prediction based on each of the modelling methods and combines them (Araújo & New, 2007). A future direction may be to create multi-climate, multi-SDM ensemble predictions.
6. One criticism that was not directly addressed in this thesis is that SDMs rely on abiotic variables whilst ignoring the biotic interactions between species (Buckley *et al.*, 2010; Guisan & Thuiller, 2005). Natural systems are a complex network of species interactions. Any change to a single species can have wide ranging effects

on others within that network. This study has incorporated habitat preferences, but does not address the predator/prey interaction as some studies are now attempting (Trainor *et al.*, 2014; Aragón & Sánchez-Fernández, 2013). The predator/prey interaction is clearly important, but the dynamics of the predator/prey relationship should be considered carefully to understand its role in defining species distributions. Typically, we consider predators and prey to fluctuate around an equilibrium based on the Lotka–Volterra model. This is expected to result in fluctuating populations of both species, but typically predation would not cause the extinction of prey species as this would lead to the extinction of the other (Begon, 2006). In studies of ungulate population crashes vegetation was the primary cause rather than predation (Owen-Smith, 2002). This suggests that predation may often not define the presence of a species, but rather limit its density.

However, other research has indicated that the predator/prey relationship is more complicated than being a simple two species interaction. Prey species are regulated by top-down and bottom-up processes, whereas predator species may be bottom-up alone (Stenseth *et al.*, 1997). For herbivores multiple predator species may influence a population, as might various species of vegetation or forage. For example, Stenseth *et al*. (1997) demonstrated that the classic hare/lynx relationship actually involves a complex food web including many predators and vegetation types, and competition for resources by both predator and prey. These complex relationships will likely prove difficult to reliably model without further research particularly for herbivores.

Predators may also influence the dispersal of species. Laboratory studies have shown that predators may cause the extinction of dispersing prey species with small population sizes. This resulted in subsequent extinction of the predator (see Begon, 2006). However, this was a simplified experiment with a single predator and prey species (two mite species) under constant conditions, whereas nature presents multiple prey and predators in a heterogeneous landscape.

A further challenge for dispersing herbivores may be interspecific competition for resources when encountering novel species (Lavergne *et al.*, 2010). Theoretical models have shown that interspecific competition can limit or narrow a species' range along environmental gradients (Case *et al.*, 2005) and field studies have also indicated that interspecific competition with related species can limit species

distributions (Cunningham *et al.*, 2009). Therefore, interspecific competition between herbivores may shape the distributions of dispersing antelope species. However, as identified in this study, currently across Africa there are areas of high antelope diversity with up to 23 sympatric species in some parts of Tanzania. These areas therefore support species with similar environmental requirements. Within these high diversity areas there are also species with similar dietary needs which suggests interspecific competition for resources may be present but does not currently restrict species from those areas. Sinclair's (1985) study supports this and shows that multiple ungulate species utilize the same plant species and have high dietary overlap, although seasonal changes and interspecific competition were present. In the same study, interspecific competition and predation were found to influence the distribution and structure of ungulate communities equally. This suggests that resources may not be the limiting factor on the presence of antelope species, but it is less clear what impact it has on the abundance of those species. Further research is required to understand the dynamics of interspecific competition, its influence on the distribution of species, and to enable its incorporation in species distribution models.

Concerns for antelope conservation in the 21st century

Identifying species of concern, areas of particular importance, and potential translocation sites in light of forecasted climatic changes is an important step in producing a cohesive conservation strategy for antelope species over the 21st century. However, other severe threats face antelopes and these must also be considered, both at their present levels and their expected levels in the future:

Human population. During the 20th century overexploitation was classified as having a high impact on tropical grassland and savannah areas, and a very high impact on tropical forests (MEA, 2005). Predictions suggest that the situation will worsen in forest areas and continue in the others during this century (MEA, 2005). Mammals, and ungulates in particular, are being depleted at unprecedented rates. The increased threat from subsistence hunting, and more recently commercial hunting, is due to improved hunting techniques, accessibility to remote areas, and a rapid increase in human population growth, all of which have become a serious threat to many wildlife populations (Fa & Brown, 2009). As the human population in Africa rapidly grows over the 21st century, there will be increasing pressure placed

on wild populations unless wildlife-friendly livelihoods can be provided. However, in forests, providing alternative sources of protein is complex as livestock productivity is low in these areas, and investment costs and risks are high, whereas bushmeat is a low cost, open access resource (Fa & Brown, 2009).

Habitat conversion. Increased urbanization is forecast to strongly impact parts of Kenya, Uganda, Rwanda, and Burundi in east/central Africa as well as coastal regions of Côte d'Ivoire, Ghana, Togo, Benin, and Nigeria by 2030 (Seto *et al.*, 2012). In addition, widespread agricultural expansion and tree cover loss is predicted across tropical Africa (van Asselen & Verburg, 2013). Agriculture, competition with livestock, and natural system modifications are already listed as threats to over half of Africa's antelope species (38 of 73; IUCN, 2014a). The combination of further loss of natural areas, larger human populations, and greater accessibility to wild areas brought about by urbanization and agriculture are likely to place unprecedented pressure on many wildlife populations.

Conflict. Chapters five and six highlighted a concern for species that are currently in areas of civil unrest or military conflict such as Somalia. Four species (beira, Speke's gazelle, dibatag and silver dik-dik) are predicted to be found only in Somalia by 2080. In these areas conservation organizations are largely helpless to provide protection. Chapter six identified climatically suitable areas beyond Somalia's borders, however, gaining access to animals for translocation projects will likely prove difficult. Speke's gazelle and beira have *ex-situ* populations which may be available for translocation projects, however dibatag and silver dik-dik are found only in the wild (IUCN, 2014a).

Fences and borders. Antelopes have no understanding of artificial borders or boundaries created by humans. Fences may delimit borders of protected areas, private game reserves, and in some cases countries. Fencing has long been used as a conservation management tool to protect against human exploitation, but its long-term effectiveness has been questioned (Massey *et al.*, 2014). Positive effects of fencing include reduced human/animal conflict, reducing road accidents, preventing disease, managing livestock conflict (see Boone & Hobbs, 2004), restricting invasive species, and reduced poaching (Hayward & Kerley, 2009; but see Massey *et al.,* 2014). However, negative effects include inbreeding through isolation, restriction of evolutionary potential, unnatural population dynamics and overabundance routes (Hayward & Kerley, 2009). They also act to curtail migration (Naidoo *et al*., 2012),

and prevent dispersal of antelopes in relation to climate change (Ogutu & Owen-Smith, 2003).

The protected area network solutions presented here incorporate groupings of existing and new protected areas that form larger areas, which benefit wildlife. In some cases this requires the development of transfrontier parks. The grouping of protected areas will require the removal of fences, potentially between neighbouring countries, if the benefits of the larger protected areas are to be realized. Furthermore, if antelope species are to naturally disperse in order to stay within suitable climatic conditions, it is likely that existing fences will need to be removed or semi-permeable fence solutions sought (Boone & Hobbs, 2004). However, the risks associated with fence removal must also be considered, particularly in relation to overexploitation consequential to poaching.

Final thoughts

Multiple threats face Africa's antelopes, and studies such as the one presented here help us to identify how threats may evolve over time. This in turn allows possible solutions to be identified, and recommendations to be made for the direction of further research with the goal of conserving these species. Specifically, by identifying species at risk, producing protected area network solutions, and indicating potential areas for assisted dispersal and migration, I here provide important data for the future development of species specific conservation efforts.

The future for antelope species across Africa remains uncertain in light of the multiple threats that they face in the next few decades. The detrimental impacts of climate change and overexploitation look set to increase as the human population rapidly expands. In addition, agricultural expansion and rapid increases in livestock production to accommodate human growth (van Asselen & Verburg, 2013) constitute severe threats to all African antelope species. However, this thesis has shown that areas of suitable climate are predicted to be present for all species; continued development of the protected area network will be needed, and some species may require translocation to ensure their survival. There is still much planning and research required if all species are to be protected for future generations to enjoy and benefit from, but ultimately, areas remain for all species and their survival remains achievable with global will and hard work.

8. Acronyms

AC	Average Contraction
ACDC	Accelerating Decelerating
AD	Assisted Dispersal
AE	Average Expansion
AIC	Akaike Information Criteria
ANN	Artificial Neural Networks
ANOVA	Analysis of Variance
AOGCM	Atmosphere-Ocean Global Circulation Models
AOO	Area OF Occupancy
ARR	Average Range Remaining
AUC	Area Under the Curve
BCCR	Bjerknes Centre for Climate Research
BCM2	Bergen Climate Model
BP	Before Present
CB-PES	Community-Based Payments for Ecosystem Services
CBC	Community-Based Conservation
CBD	Convention on Biological Diversity
CBNRM	Community-Based Natural Resource Management
CC	Climate Change
CCSM3	Community Climate System Model
CEC	Cation Exchange Capacity
CEM	Climate Envelope Models
CH_4	Methane
CO_2	Carbon Dioxide
CR	Critically Endangered
CTA	Classification Tree Analysis
DRC	Democratic Republic of Congo
EB	Early Burst
EEA	European Environment Agency
EN	Endangered
ENM	Environmental Niche Model
ENSO	El Niño/Southern Oscillation
EOO	Extent of Occurrence
EW	Extinct in the Wild
EX	Extinct
FP	Final Probability
GAM	Generalized Additive Models
GDP	Gross Domestic Product
GHG	Greenhouse Gases
GIS	Geographic Information Systems
GLM	Generalized Linear Models
GR	Game Reserve
HADCM3	Hadley Centre Coupled Model
HP	High Protection
HWSD	Harmonized World Soil Database
ICDP	Integrated Conservation and Development Projects
IP	Initial Probability

IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for the Conservation of Nature
LC	Least Concern
LP	Low Protection
LT	Land Transformation
KAZA	Kavango-Zambezi Transfrontier conservation Area
KNT	Kenya, Namibia, and Tanzania
MARS	Multivariate Adaptive Regression
MAXENT	Maximum Entropy
MDA	Mixture Discriminant Analysis
MEA	Millennium Ecosystem Assessment
ML	Maximum Likelihood
NCAR	US National Centre for Atmospheric Research
NDVI	Normalized Difference Vegetation Index
NGO	Non-Governmental Organization
NP	National Park
NT	Near Threatened
OMI	Outlying Mean Index
OU	Ornstein-Uhlenbeck
PA	Protected Area
PAN	Protected Area Network
PCA	Principal Components Analysis
PET	Potential Evapotranspiration
pgls	Phylogenetic Generalized Least Squares
ppm	Parts per-million
RF	Random Forest
ROC	Receiver Operating Characteristic
s.d.	Standard Deviation
SDM	Species Distribution Model
SRE	Surface Range Envelope
UKMO	United Kingdom Met Office
UNEP	United Nations Environment Programme
UNFCCC	United Nations Framework Convention on Climate Change
USDA	United States Department of Agriculture
USGS	United States Geological Survey
VU	Vulnerable
WDPA	World Database of Protected Areas

9. General appendix

	Scientific Name	English Name
1	*Addax nasomaculatus*	Addax
2	*Aepyceros melampus*	Impala
3	*Alcelaphus buselaphus*	Hartebeest
4	*Ammodorcas clarkei*	Dibatag
5	*Antidorcas marsupialis*	Springbok
6	*Beatragus hunteri*	Hirola
7	*Cephalophus adersi*	Aders' duiker
8	*Cephalophus callipygus*	Peters' duiker
9	*Cephalophus dorsalis*	Bay duiker
10	*Cephalophus harveyi*	Harvey's duiker
11	*Cephalophus jentinki*	Jentink's duiker
12	*Cephalophus leucogaster*	White-bellied duiker
13	*Cephalophus natalensis*	Natal Red duiker
14	*Cephalophus niger*	Black duiker
15	*Cephalophus nigrifrons*	Black-fronted duiker
16	*Cephalophus ogilbyi*	Ogilby's duiker
17	*Cephalophus rufilatus*	Red-flanked duiker
18	*Cephalophus silvicultor*	Yellow-backed duiker
19	*Cephalophus spadix*	Abbott's duiker
20	*Cephalophus weynsi*	Weyns' duiker
21	*Cephalophus zebra*	Zebra duiker
22	*Connochaetes gnou*	Black wildebeest
23	*Connochaetes taurinus*	Common wildebeest
24	*Damaliscus lunatus*	Topi
25	*Damaliscus pygargus*	Blesbok/bontebok
26	*Dorcatragus megalotis*	Beira
27	*Eudorcas rufifrons*	Red-fronted gazelle
28	*Eudorcas thomsonii*	Thomson's gazelle
29	*Gazella cuvieri*	Cuvier's gazelle
30	*Gazella dorcas*	Dorcas gazelle
31	*Gazella leptoceros*	Slender-horned gazelle
32	*Gazella spekei*	Speke's gazelle
33	*Hippotragus equinus*	Roan antelope
34	*Hippotragus niger*	Sable antelope
35	*Kobus ellipsiprymnus*	Waterbuck
36	*Kobus kob*	Kob
37	*Kobus leche*	Southern Lechwe
38	*Kobus megaceros*	Nile Lechwe
39	*Litocranius walleri*	Gerenuk
40	*Madoqua guentheri*	Guenther's dik-dik
41	*Madoqua kirkii*	Kirk's dik-dik
42	*Madoqua piacentinii*	Silver dik-dik

43	*Madoqua saltiana*	Salt's dik-dik
44	*Nanger dama*	Dama gazelle
45	*Nanger granti*	Grant's gazelle
46	*Nanger soemmerringii*	Soemmerring's gazelle
47	*Neotragus batesi*	Bates' Pygmy antelope
48	*Neotragus pygmaeus*	Royal antelope
49	*Nesotragus moschatus*	Suni
50	*Oreotragus oreotragus*	Klipspringer
51	*Oryx beisa*	Beisa Oryx
52	*Oryx dammah*	Scimitar-horned Oryx
53	*Oryx gazella*	Gemsbok
54	*Ourebia ourebi*	Oribi
55	*Pelea capreolus*	Grey Rhebok
56	*Philantomba maxwellii*	Maxwell's duiker
57	*Philantomba monticola*	Blue duiker
58	*Raphicerus campestris*	Steenbok
59	*Raphicerus melanotis*	Cape grysbok
60	*Raphicerus sharpei*	Sharpe's grysbok
61	*Redunca arundinum*	Southern reedbuck
62	*Redunca fulvorufula*	Mountain reedbuck
63	*Redunca redunca*	Bohor reedbuck
64	*Sylvicapra grimmia*	Common duiker
65	*Syncerus caffer*	African Buffalo
66	*Tragelaphus angasii*	Nyala
67	*Tragelaphus buxtoni*	Mountain Nyala
68	*Tragelaphus derbianus*	Giant Eland
69	*Tragelaphus eurycerus*	Bongo
70	*Tragelaphus imberbis*	Lesser Kudu
71	*Tragelaphus oryx*	Common Eland
72	*Tragelaphus scriptus*	Bushbuck
73	*Tragelaphus spekii*	Sitatunga
74	*Tragelaphus strepsiceros*	Greater Kudu

Appendix 9-1: List of antelope species modelled with both scientific and English names. Oryx dammah was removed due to a poor performing model (see chapter three methods and discussion).

USGS conversions

Value	USGS Description	Recode
1	Fir/Cedar Forest	1
2	Atlantic Coast Dry Forest	2
3	Secondary Semi-deciduous Forest/Woodland	1
4	Tropical Plantations	2
5	Tropical Rainforest	1
6	Tropical Rainforest	1
7	Secondary Tropical Lowland Forest with Mangroves	1
8	Open And Fragmented Forest	2
9	Tropical Rainforest with Savannah	2
10	Tropical Rainforest	1
11	Sclerophyllous Forest (Deciduous and Evergreen Oak)	1
12	Tropical Rainforest with Savannah	2
13	Tropical Rainforest	1
14	Tropical Plantations (Rubber, Coffee, Tea)	1
15	Miombo Woodland and Shrubland	2
16	Montane Evergreen Forests	1
17	Evergreen Broadleaf Forest	2
18	Miombo Woodland	2
19	Montane Evergreen Forest	1
20	Tropical Rainforest	1
21	Miombo Woodland	2
22	Low Open Forest/Woodland	2
23	Miombo Woodland/Forest	2
24	Tropical Forest	1
25	Tropical Rainforest	1
26	Secondary Tropical Forest	2
27	Tropical Rainforest	1
28	Humid Tropical Forest	1
29	Tropical Forest with Semi-Deciduous Element	1
30	Tropical Forest/Miombo Woodland	1
31	Tropical Broadleaf Evergreen Rainforest	1
32	Tropical Broadleaf Evergreen Rainforest	1
33	Montane Broadleaf Evergreen Forest	1
34	Broadleaf Semideciduous Forest	1
35	Montane Broadleaf Evergreen Woodland	1
36	Dense Tropical Rainforest	1
37	Tropical Forest with Semi-Deciduous Element	1
38	Dry Deciduous Forest with Grassland	2
39	Conifer And Bamboo	1
40	Open Montane Forests Mixed With Bamboo	1
41	Subtropical Forest, Forest Plantation	1
42	Sclerophyllous Scrub with Cereal Crops	2
43	Acacia Bushland/Thicket	2
44	Acacia Bushland/Thicket	2
45	Sclerophyllous Scrub/Woodland	2
46	Acacia Bushland/Thicket	2
47	Bushland and Thicket	2
48	Sclerophyllous Scrub with Cereal Crops	2
49	Bush Woodland	2
50	Acacia Bushland Thicket	2
51	Schlerophyllous Scrub/Woodlands	2
52	Acacia Bushland/Thicket	2
53	Cropland/Degraded Forest Savannah	2
54	Desert Shrubland/Grassland	2
55	Desert Shrubland/Grassland	2
56	Desert Shrubland/Grassland	2
57	Desert Shrubland/Grassland	2
58	Bush/Shrubland	2

59	Annual Grass and Sahel Shrub	2
60	Acacia Shrubland/Grassland	2
61	Desert with Succulent Shrubs	2
62	Acacia Bush/Thornland Thicket	2
63	Desert/Hammadas/Shrubland	2
64	Semi-Desert Shrubland with Grassland	2
65	Shrubland with Grassland	2
66	Acacia Bushland/Thickets	2
67	Shrubland with Grassland	2
68	Semi-Desert Shrubland with Grassland	2
69	Acacia Shrubland/Bushland	2
70	Bushland and Thicket	2
71	Dry Deciduous Forest/Grassland Mosaic	2
72	Bamboo, Plantations	1
73	Sudanian Woodland with Crops	1
74	Atlantic Evergreen Broadleaf, Lowland Dry Woodland	1
75	Transitional Forest/Sudanian Woodland	1
76	Sudanian Dry Woodland	1
77	Grassland/Woodland Mosaic	2
78	Tree Savannah	2
79	Tree Savannah	2
80	Degraded Forest/Savannah with Cropland	2
81	Miombo Woodland And Woody Plantations	2
82	Evergreen Broadleaf Woodland	1
83	Savannah/Miombo Woodland	2
84	Woody Savannah	2
85	Sudanian Woodland	1
86	Dense Sudanian Woodland with Grassland	2
87	Miombo Woodland	2
88	Sudanian Woodland	1
89	Sudanian Woodland	1
90	Woody Savannah Degraded From Dry Forest	2
91	Woodland, Woody Savannah	2
92	Woodland, Woody Savannah	2
93	Grassland/Sudanian Woodland	2
94	Sudanian Woodland/Savannah	2
95	Sudanian Woodland/Savannah	2
96	Deciduous Thicket/Grassland Mosaic	2
97	Scrub Woodland Or Tree Savannah	2
98	Sudanian Woodland with Crops	2
99	Savannah	2
100	Shrub Savannah	2
101	Woodland/Grass/Shrub Mosaic	2
102	Montane Dry Sparse Forest/Grassland	2
103	Savannah	2
104	Savannah	2
105	Savannah	2
106	Savannah	2
107	Low Shrub - Bushland Savannah with Cropland	2
108	Savannah with Cropland	2
109	Woodland/Acacia/Grassland Mosaic	2
110	Woodland/Grassland Savannah	2
111	Savannah	2
112	Savannah with Cropland	2
113	Scrub Woodland Or Tree Savannah	2
114	Low Shrub - Bushland Savannah (Degraded from Miombo Woodland with Fire Burns)	2
115	Open Miombo Woodland With Improved Grassland	2
116	Sudanian Woodland/Savannah	2
117	Deforested Savannah with Crops	2
118	Savannah	2
119	Low Shrub Bushland with Cropland	2

120	Semi-Desert Grassland with Shrubland	2
121	Grassland/Shrubland	2
122	Grassland/Shrubland	2
123	Grassland/Shrubland	2
124	Grassland with Acacia Bushland	2
125	Grassland with Woodland	2
126	Grassland/Acacia Shrubland with Cropland	2
127	Grassland with Shrubland	2
128	Grassland, Herbaceous Wetland	2
129	Grassland/Shrubland	2
130	Grassland With Cropland	2
131	Shrubland/Grassland with Cropland	2
132	Grassland/Shrubland	2
133	Grassland with Cropland,Wetland	2
134	Mangroves/Swamps, Tropical Forest	1
135	Mangroves/Swamps, Tropical Forest	1
136	Mangroves	1
137	Deforested Coastal, Mangrove	2
138	Herbaceous Wetlands (Sud)	2
139	Herbaceous With Woody Wetlands (Okavanga Swamp)	2
140	Cropland with Shrubland	3
141	Cropland (Peanuts) with Baobab/Acacia	3
142	Cropland (Rice)	3
143	Cropland (Rice, Peanuts)	3
144	Cropland with Wetland	3
145	Cropland (Corn, Grains)	3
146	Pasture/Cropland	3
147	Nonirrigated Cropland	3
148	Pasture/Cropland	3
149	Cropland (Cereals, Pasture)	3
150	Cropland,Vineyards,Orchards	3
151	Cropland (Sugar Cane And Other Crops)	3
152	Shifting Agriculture, Tea, Tobacco	3
153	Nonirrigated Cropland (Cereals, Pasture)	3
154	Cropland	3
155	Cropland with Grassland Savannah	3
156	Cropland	3
157	Cropland with Grass	3
158	Cropland with Woody Plantations	3
159	Pasture/Cropland with Orchards	3
160	Cropland	3
161	Cropland with Sclerophyllous Forest	3
162	Agriculture Plantations	3
163	Irrigated Agriculture	3
164	Cropland with Tropical Forest	3
165	Cropland	3
166	Agriculture Plantations	3
167	Cropland (Tea/Coffee Plantations)	3
168	Cropland	3
169	Grassland/Cropland	3
170	Sudanian Woodland/Agriculture Mosaic	4
171	Shrubland/Irrigated Crops/Tree Crops	4
172	Cropland/Savannah/Bushland Mosaic	4
173	Degraded Tropical Forest/Cropland	4
174	Grassland/Cropland (Wheat,Small Grains)	4
175	Tropical Forest/Cropland Mosaic	4
176	Cropland/Plantations/Savannah Mosaic	4
177	Cropland/Woodland Savannah	4
178	Cropland (Plantations)/Woodland	4
179	Cropland/Savannah Mosaic	4
180	Secondary Tropical Forest/Cropland	4

181	Secondary Tropical Forest/Cropland	4
182	Cropland/Shrubland	4
183	Cropland/Miombo Woodland	4
184	Savannah/Cultivated Crops	4
185	Cropland/Savannah Mosaic	4
186	Woodland/Cropland	4
187	Secondary Forest/Cropland	4
188	Cropland/Fruit/Vineyards/Secondary Forest	4
189	Fragmented Dry Forest, Fallow, Cultivation	4
190	Cropland/Tropical Forest	4
191	Barren Or Sparsely Vegetated	2
192	Sahara/Sahel Sparsely Vegetated	2
193	Barren Or Sparsely Vegetated	2
194	Sahara/N. Sahel Sparsely Vegetated	2
195	Sparse Sahel Shrubs/Sahara Hammadas	2
196	Inland Water	3
197	Ocean	3

Appendix 9-2: Recoding of 197 USGS habitat types to 1=Closed, 2=Open, 3=Human dominated, 4=Not found in Africa. These are used by the habitat filter where it is applied. Specialist species can only disperse in suitable habitat. Nothing can disperse into or through human dominated habitat.

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